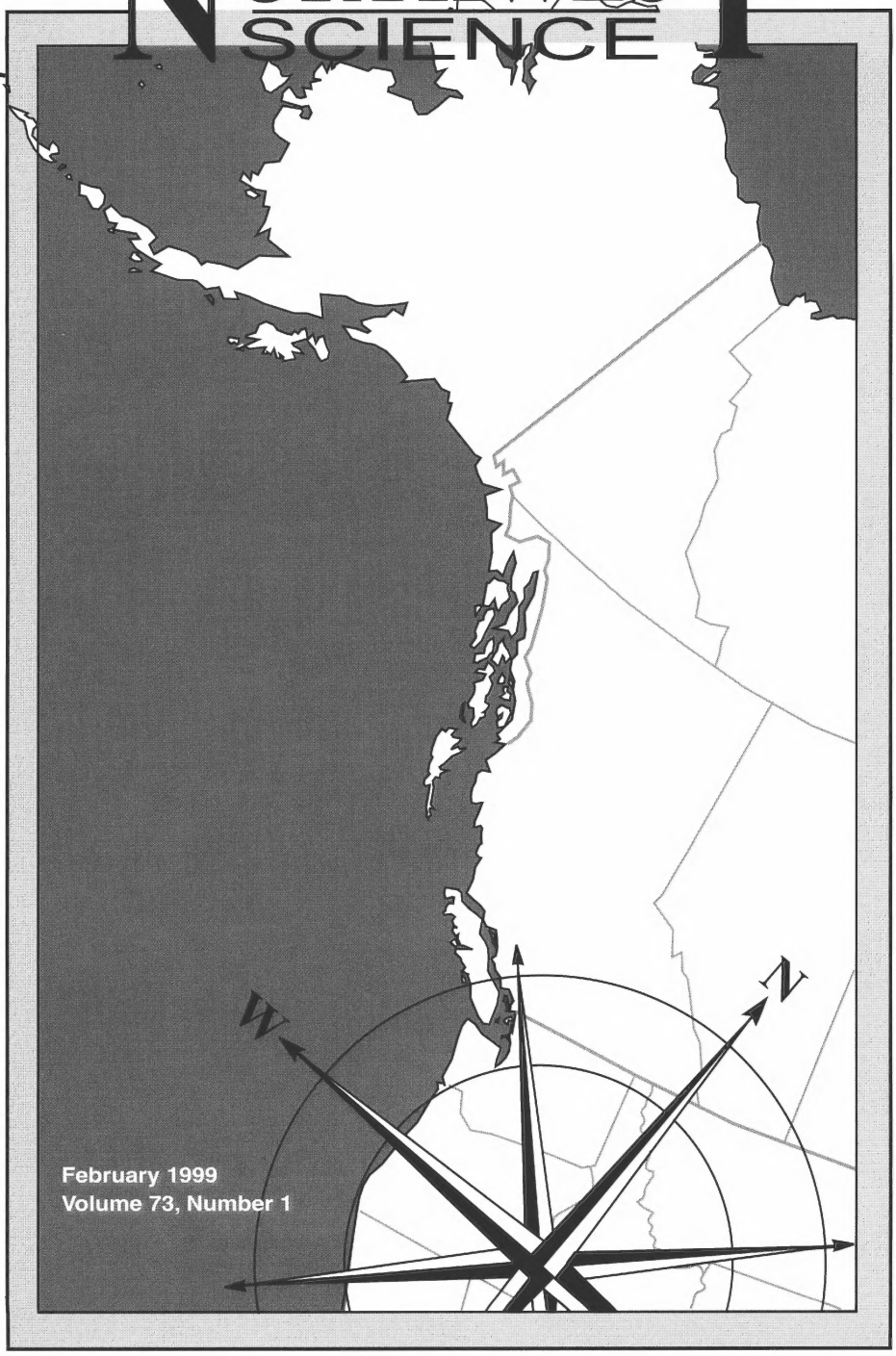
NORTHWEST SCIENCE



February 1999
Volume 73, Number 1

Northwest Scientific Association

(Founded 1923)

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The Northwest Scientific Association is a 501-C(3) tax status organization.

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February 1999 Volume 73, Number 1

NORTHWEST SCIENCE

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ISSN #0029-344X

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Announcements

Associate Editor for Aquatic Biology

Dr. Gary Larson is stepping down as Associate Editor for Aquatic Biology after nearly 10 years. Gary, please accept our sincere thanks for your many years of excellent service and numerous reviews. You have contributed substantially toward our goal of publishing high-quality articles in *Northwest Science.* We wish you well in all your new endeavors. Our new Associate Editor for Aquatic Biology is Dr. Ross Black, Eastern Washington University. We appreciate your willingness to accept these new responsibilities. Welcome aboard, Ross!

Errata

The following erratum is printed at the request of Craig Delong. It refers to the paper "Natural Disturbance Rate and Patch Size Distribution of Forests in Northern British Columbia: Implications for Forest Management" which appeared in *Northwest Science* Volume 72: Special Issue on Fire, Pages 35-48.

> "There was an contextual error on page 36 of this paper. The following references Vasbinder et al. 1997 and Hawkes et al. 1997 were placed along with other papers it was indicated showed no evidence they were intended to assist in the development of more ecologically based forest. This is not the case with these 2 studies which were part of research conducted as part of the McGregor Model Forest project which was intended to develop sustainable forest management practices for the area."

It has also been noted that the wrong Figure 1 was printed in the the paper "Long-term Fire Incidence in Coastal Forests of British Columbia" by Kendrick J. Brown and Richard J. Hebda which appeared in *Northwest Science* Volume 72: Special Issue No. 2, Pages 64-66. I apologize to the authors for any inconvenience this has caused. The entire paper is reprinted in this issue (pp. 41-43).

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Landscape and Patch Scale Habitat Use by Migratory Black-tailed Deer in the Klickitat Basin of Washington

Abstract

I studied habitat use of Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in the Klickitat Basin of Washington. The habitat mosaic for Klickitat deer consisted of large tracts managed independently by the Yakama Indian Nation, the State of Washington, and two corporate forest-owners. Selection of habitats at the landscape and patch scale was investigated using radiocollared deer. During winter, deer preferred habitats with an overstory dominated or codominated by Oregon white oak (*Quercus garryanna*) at both scales of selection. Also during winter, deer selected home ranges with less mixed conifer cover type than available in the background mosaic, but showed some preference for mixed conifer patches within home ranges. Deer occupying mid-elevation home ranges on the Yakama Reservation preferred mature/old-growth and younger, closed-canopy conifer stands at both selection scales during summer. Mid-elevation deer on corporate forestland summer range preferred mature/old-growth stands and open-canopy conifer stands at the landscape scale and the same two habitat classes in reverse order at the patch scale. During summer, deer with high elevation home ranges used habitats in relative proportion to their availability at both selection scales. Habitat conservation for Klickitat deer is complicated by a mixed-ownership mosaic and diverse management approaches. Private land habitat values are important during summer and winter, and conservation may require extensive coordination between public and private resource managers and incentives for private landowners. Conservation of oak-dominated habitat on winter range and mature and old-growth habitat on summer range should be a priority for Klickitat deer managers.

Introduction

Knowledge of a species' habitat affinities is essential to informed management. For example, without basic knowledge of habitat relationships, the consequences of habitat alteration resulting from human land uses cannot be predicted nor can cover types be ranked according to their value. Previous studies have documented some aspects of habitat use for Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in mesic habitats of their range (Brown 1961, Miller 1970, Loft et al. 1984, McNay et al. 1994). However, little is known about black-tailed deer habitat use along the eastern edge of their distribution where the more xeric environment supports different vegetation than in coastal and westslope habitats.

During 1988-94, I studied the ecology of migratory black-tailed deer in the Klickitat River Basin (KRB) along the eastslope of the Washington Cascades. In this paper, I report on habitat use patterns of KRB deer, which were studied in a mixed-ownership landscape managed by the Yakama Indian Nation, the state of Washington, and two large forest products companies.

Conceptually, I addressed habitat relationships at two levels of selection: (1) selection of home ranges from a background habitat mosaic (landscape-scale selection), and (2) selection of habitat patches within the seasonal home ranges of individual deer (patch-scale selection). Specifically, the following null hypothesis was tested for both wintering and summering KRB deer relative to landscape selection: cover types within deer home ranges were proportional to their availability in a broader habitat mosaic. The null hypothesis tested for wintering and summering KRB deer relative to patch selection was: deer used cover types proportionally to their availability within home ranges.

Study Area

Physiography and Climate

The KRB consists of approximately 350,000 ha of forest and rangeland along the eastern slope of the Washington Cascades (Figure 1). Elevations range from 3,742 m at the crest of Mt. Adams to less than 600 m. The upper basin lays mostly within the 650,000 ha Yakama Indian Reservation. Topographically, the upper basin is characterized by rugged, mountainous country along the Cascade crest that quickly grades into a large, forested plateau. Except for the highly dissected

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Klickitat River Canyon, most of this plateau consists of a gently rolling basin that eventually rises to form the Simcoe Mountains along the southern boundary of the Yakama Reservation. Favorable physiographic conditions for wintering deer exist along the lower slopes of the Simcoe Mountains. The lower, southern-most portions of the KRB historically consisted of discontinuous coniferous forest, Oregon white oak (*Quercus garryanna*) woodlands, and rangeland. Considerable agricultural and rural development has occurred in the lower reaches of the drainage near the towns of Goldendale and Glenwood.

Annual precipitation ranges from nearly 180 cm to approximately 20 cm, depending on elevation and distance from the Cascade Mountains. Precipitation is strongly seasonal with most falling during winter and spring. Mean annual snowfall measured in nearby Yakima, Washington, 1964-94, was 61.2 cm (National Oceanic and Atmospheric

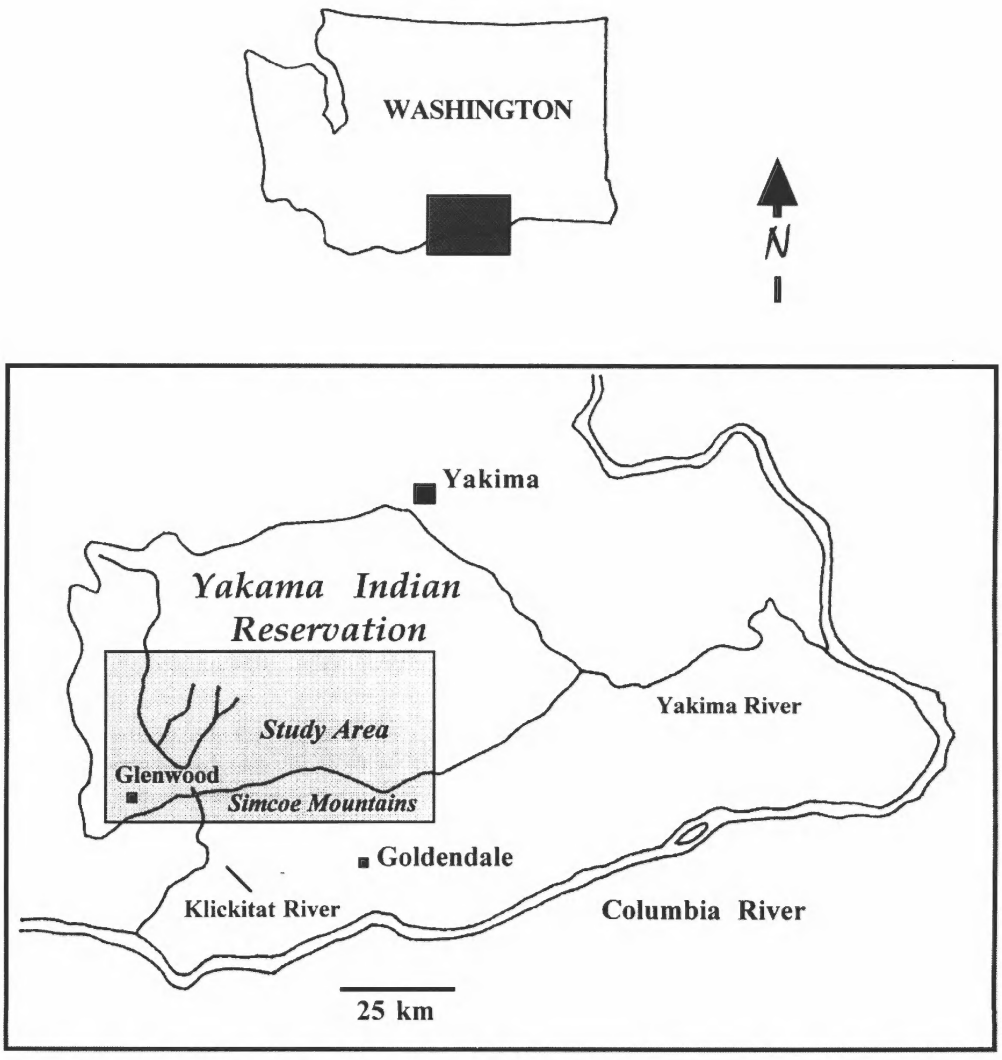

Figure 1. Location of the Klickitat Basin and Yakama Indian Reservation, Washington.

Administration [NOAA] 1994). During this study (1988-94), annual snowfall was below this long-term mean during the winters of 1988-89, 1989-90, 1990-91, 1991-92, and 1993-94 (NOAA 1994). Annual snowfall exceeded the 1964-94 mean during winter 1992-93 and was the second highest snowfall recorded since 1910.

Vegetation

Habitats of the upper Klickitat are primarily alpine and subalpine communities dominated by mountain hemlock (*Tsuga mertensiana*), Pacific silver fir (*Abies amabilis*), and subalpine fir (*A. lasiocarpa*) associations (John et al. 1988). Mid-elevation mixed-conifer stands are dominated by western hemlock (*T. heterophylla*), grand fir (*A. grandis*), and Douglas-fir (*Pseudotsuga menziesii*). Lower elevation forests are typically dominated by ponderosa pine (*Pinus ponderosa*) associations. The forest/rangeland ecotone is characterized by mixed ponderosa pine/Oregon oak stands or pure Oregon oak woodlands.

Nonforested habitats include abundant wet meadow and subalpine park areas in the upper KRB and widespread xeric meadows and shrubfields at lower elevations. Rangeland habitats are dominated by perennial grasses such as bluegrasses (*Poa* spp.) and fescues (*Festuca* spp.) and discontinuous shrub overstories dominated locally by sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and shiny-leaf ceanothus (*Ceanothus velutinus*).

Habitat Management

About 200,000 ha of the KRB is within the Yakama Reservation. Boise Cascade Corporation owns approximately 30,000 ha of mid-elevation forest in the KRB, and Champion International Corporation owns an additional 38,000 ha of KRB forest land, most in the western part of the drainage. Additionally, the Washington Department of Natural Resources manages approximately 19,000 ha of state forest land south of the Yakama Reservation. Reservation lands in the KRB provide summer range, whereas state and private lands south of the reservation provide a mix of summer and winter range.

Commercial forest management is the dominant land use in the KRB. Yakama Reservation forests have been managed using uneven-aged management for several decades; clearcutting on the reservation has historically been rare (McCorquodale et al. 1997). Clearcutting and intensive selective harvesting has been more extensive on corporate and state-owned timberlands in the KRB. Other land uses include cattle grazing, common on both reservation and corporate timberlands, and agricultural development in the lower Klickitat.

Deer winter range in the lower Klickitat consists of a series of south-facing breaks along the Klickitat River canyon. These open slopes rise steeply from extensive forest stands along the river. As the breaks grade into the lower Simcoe plateau, these openings give way to oak woodlands, and eventually to extensive pine forest as distances from the river and elevations increase. Forest cover, both coniferous and deciduous, is extensive on some portions of the Klickitat winter range.

Methods

Marking and Telemetry

Deer were captured using collapsible Clover deer traps (McCullough 1975) and a hand-triggered, 21 m x 21 m drop net (Ramsey 1968, Conner et al. 1987). Trapping was conducted after the close of recreational hunting seasons, and typically occurred between mid-December and late-February. Traps were dispersed throughout the winter study area in all major cover types to avoid biasing the collection of habitat use data. A sample of adult deer captured each year received radiocollars (MOD-500, Telonics, Inc., Mesa, Arizona). Although I did not use a formal randomization protocol, I attempted to spread radiocollars throughout the winter study area, thus avoiding the oversampling of specific matrilines. Most radios were placed on adult female deer, but some were placed on adult males. Radios transmitted at 148-150 Mhz and had an estimated two to three year battery life.

Radiocollared deer were relocated weekly during spring, summer, and fall, and approximately twice monthly during winter. Relocations were obtained from a Cessna 182 or Citabria aircraft fitted with two strut-mounted directional antennas. Aerial tracking protocol generally followed that of Gilmer et al. (1981). Coordinates for aerially-relocated deer were determined using a Geographic Positioning System (GPS) unit mounted on the aircraft's instrument panel.

Coordinates obtained from the GPS unit were converted from latitude and longitude to Universal Transverse Mercator (UTM) coordinates using a computer algorithm (Dodge et al. 1986). Periodically, GPS accuracy was tested by collecting coordinates for known locations.

Movements and Home Range Estimation

Seasonal home ranges (100% minimum convex polygon [MCP]) for radiocollared deer were estimated with PROGRAM HOME RANGE (Ackerman et al. 1989). Minimum Convex Polygon estimates were used to facilitate habitat analyses because they were nonparametric, required few assumptions, and were simple to map using a Geographic Information System (GIS). My interest in home ranges was primarily to define sampling units for habitat questions. Inter-year seasonal home range overlap for deer that were tracked for more than one year was considered evidence of home range fidelity. Inter-year relocation data were pooled for seasonal home range estimation in cases where home range fidelity was documented. Seasonal home ranges were estimated only for deer with at least 10 seasonal relocations.

Habitat Use Relationships

Preliminary observations suggested that KRB deer summered in a diverse array of cover types in environments ranging from subalpine to oak/shrub-steppe ecotone. During winter, however, deer in the KRB regularly concentrated in a narrow range of habitats. Because of this, the analytical strategy differed for summer and winter deer habitat use data.

During winter, the proportional composition of home ranges and the proportional use of cover types by radiocollared deer were examined in a GIS environment (ArcInfo®). Statistical testing of habitat use hypotheses was based on rank testing using the methods of Johnson (1980) and Friedman (1937). The 2 methods differ subtly. The Johnson method is based on the difference in the ranks of used and available habitats accross all individuals. In contrast, in the Friedman approach, the difference in the proportions of available and used habitats is calculated for each individual and these computed differences are then ranked within individuals. Rank-testing approaches had two distinct advantages over other methods: (1) small errors in estimating habitat availabilities were inconsequential, and (2) by maintaining individual-level telemetry data the problems associated with pooling data from different individuals was avoided (Alldredge and Ratti 1986). However, these methods still facilitate inference about population-wide patterns of resource selection (Alldredge and Ratti 1986).

I assumed that all radiocollared deer on the core winter study area had the opportunity to select (landscape scale) from the same array of available habitat components. Therefore, landscape-scale winter habitat availabilities were determined within a digitized ArcInfo® polygon that roughly corresponded to a composite winter home range of radiocollared deer, and the area of various cover types within the composite winter home range was determined using GIS.

For winter landscape-scale analyses, each deer's home range polygon was digitized using GIS, but each was enlarged by a 100 m buffer because of the way individual relocations were treated (described in next paragraph). The relative area of different cover types within individual home range polygons and within the previously-described composite winter home range polygon were then compared.

Winter deer use (patch-scale) was sampled using an ArcInfo® coverage created from winter deer telemetry locations. A relocation coverage for each deer was created by adding a 100 m circular buffer to all telemetry relocations. Each relocation was subsequently treated as a 3.14 ha circular habitat use plot centered on the original telemetry location. By using this approach, I recognized telemetry and mapping errors associated with each relocation. I also hypothesized that deer perceive and select habitats as patches rather than as points. The deer-use coverages were then modified by intersecting the buffered relocations, resulting in a final coverage of winter use for each individual. Habitat proportions were then compared between the winter use coverages and the buffered home range polygons of individual radiocollared deer according to the method of Johnson (1980).

In contrast with winter, during summer, deer were widely dispersed in a broad array of habitat associations. To prevent use of diverse mosaics by individual deer from obscuring patterns of resource selection on summer range, I classified

radiocollared deer into one of two discrete "ecogroups": (1) deer that summered at mid-elevations, primarily in habitats within ponderosa pine and mixed-conifer forest associations, and (2) deer that summered at high elevations (>1,370 m), primarily within moist mixed-conifer associations and subalpine habitats of the true fir and mountain hemlock forest associations. Patterns of resource selection were evaluated independently for these two ecogroups. The analysis of summer habitat use by Klickitat deer was further stratified by analyzing summer deer use of reservation lands separate from deer use of corporate lands outside of the reservation. The justification for this was the historical difference in KRB forest management approaches wherein uneven-aged management was applied on reservation lands and even-aged management predominated on adjacent state and private lands.

Digitized coverages of buffered point relocations and individual home range polygons for summering deer were created similarly to those for wintering deer. Evaluations of patch-scale habitat selection followed the same conceptual approach as that employed for winter analyses, except that hypothesis testing was based on the method of Friedman (1937). I used this method instead of the Johnson (1980) approach for summer deer use because tied ranks resulting from non-use of some components were a problem with some deer during summer, and the Friedman (1937) technique largely eliminated tied ranks.

Evaluations of landscape-scale selection on summer range differed slightly from that employed for winter use, because deer were not geographically concentrated within a narrow range of environments during summer. Therefore, the assumption that all deer were selecting home ranges from the same background mosaic during summer did not seem appropriate. I selected habitat adjacent to each individual deer's summer home range polygon as representing the background habitat mosaic from which home ranges were selected. Habitat availabilities were determined within a 3 km buffer adjacent to the respective 100% MCP home range, and habitat composition within home range polygons and within the 3 km buffer zones were compared to assess landscape scale selection. The Friedman (1937) method was also used to evaluate use of cover types at the landscape scale for the reasons described above.

Results

Capture and Marking

During 1988-94, radiocollars were placed on 69 deer (56 adult females and 13 adult males). The 69 radiocollared deer were collectively relocated 3,152 times. The number of radiocollared deer tracked each year varied from 16 (1989) to 44 (1991). GPS error averaged 29.8 m ± 4.8 m (1 *SE*) during accuracy tests. Actual tracking error was estimated to be <200 m for most relocations based on tracking of mortalities and test transmitters. Therefore, tracking system error (relocation error + GPS error) was estimated to average <250 m and rarely exceed 350 m.

Home Ranges

Of the 69 deer radiocollared, three died during their winter of marking without providing enough data to estimate home ranges. Of the remaining 66 deer, nine were non-migratory residents of the lower KRB where winter trapping was conducted. Resident deer were excluded from the habitat analyses because the study objectives focused on migratory deer behavior. Among migrants, the requisite number of relocations were obtained to justify estimating seasonal home ranges for 43 adult female deer during summer and 31 adult females during winter. For females, the mean number of relocations used to estimate summer and winter home ranges was 34.1 and 21.0, respectively. Summer home ranges were also estimated for eight migratory, adult males from a mean number of 22.4 relocations. Too few males were tracked to allow comparisons of habitat use between the sexes, so data from males and females were pooled for habitat analyses. Data on home range sizes and other movement parameters have been published elsewhere (McCorquodale, *in press*).

Habitat Use Relationships

Winter Habitat Relationships

Mean differences between ranks of use and availability of cover types in the background habitat mosaic during winter suggested that deer selected home ranges with more oak woodland habitat than the background mosaic (Table 1); this cover type was significantly preferred ($P < 0.05$) over all other cover types at the landscape scale. Deer home

TABLE 1. Results of winter cover-type use analyses based upon rank testing (Johnson 1980) for radiocollared Klickitat Basin black-tailed deer.

Cover Type	Available (ha)	Mean Use Deviation[a]	Preference Rank[b]
	Landscape Scale		
Open	2,085.6	- 0.12	$3^{c,d}$
Oak Woodland	1,482.3	- 1.08	$1^{c,e,f}$
Pine / Oak	4,017.2	- 0.60	$2^{e,g}$
Mixed Conifer	4,577.5	1.80	$4^{d,f,g}$
	Patch Scale		
Open	36.37	0.36	$4^{c,d,e}$
Oak Woodland	34.12	-0.20	1^{c}
Pine / Oak	141.81	-0.04	3^{d}
Mixed Conifer	64.87	-0.12	2^{e}

[a]Average deviation of ranks [use - availability] for all radiocollared deer.

[b]Overall rank of preference [1 = most preferred] [ranks denoted by shared superscript are significantly different, $P < 0.05$].

ranges also contained less mixed conifer habitat than the background mosaic during winter. Within radiocollared deer winter home ranges, moderate selection, evidenced by negative mean use deviations between the availability and proportional use of patches, was noted for oak woodland, mixed conifer, and pine/oak. Significant selection ($P < 0.05$) was not detected among these cover types, but all three were preferred over nonforested habitat patches.

Summer Habitat Relationships

The null hypothesis that deer used cover types proportional to their availability was rejected for mid-elevation ecogroup deer on reservation and nonreservation lands at the landscape scale ($T_2 = 3.23$, $T_2 = 3.43$, $P < 0.10$). Similarly, selection of habitat patches within home ranges was nonrandom for mid-elevation ecogroup deer on both reservation and nonreservation summer ranges ($T_2 = 5.29$, $T_2 = 3.08$, $P < 0.10$). At the landscape scale, home ranges of mid-elevation deer on tribal lands generally contained more mature/old-growth stands and younger, closed-canopy conifer stands than background mosaics (Table 2). At the patch scale, these deer also preferred mature/old-growth and younger, closed canopy conditions relative to nonforested and open-canopy stands (Table 2).

TABLE 2. Results of summer cover-type use analyses based upon ranks of differences between use and availability (Friedman 1937) for mid-elevation ecogroup, radiocollared Klickitat Basin black-tailed deer summering on Yakama Reservation land (n=18).

Cover Type[a]	Mean Availability	Ranks Sums (U-A)[b]	Preference Rank[c]
	Landscape Scale		
Open / shrub	0.08	57.0	$4^{d,e}$
Open conifer	0.07	48.0	3
Closed conifer	0.18	39.0	2^{e}
Mature / Old growth	0.67	37.0	1^{d}
	Patch Scale		
Open / shrub	0.05	54.0	$3.5^{d,e}$
Open conifer	0.06	54.0	$3.5^{f,g}$
Closed conifer	0.24	41.5	$2^{d,f}$
Mature / Old growth	0.65	30.5	$1^{e,g}$

[a]Open / shrub = non-forested; open conifer = ≤ 39% canopy closure (CC); closed conifer = ≥ 40% CC, < 9 in. dbh; mature / old growth = ≥ 40% CC, > 9 in. dbh.

[b]Sum of ranks of differences in use and availability percentages for all radiocollared deer.

[c]Overall rank of preference [1 = most preferred] [ranks denoted by shared superscript are significantly different, $P < 0.10$].

Mid-elevation ecogroup deer summering on private forest land also selected home ranges with more mature/old-growth than available in background mosaics; this cover type was preferred over all other cover types (Table 3). Summer home ranges of these deer also generally contained more open-canopy conifer stands than the background mosaics. Deer in this ecogroup appeared to select home ranges with less nonforested habitat than was typical of background mosaics. Within the summer home ranges of these deer, preference was noted for open-canopy conifer habitat and mature/old-growth, and non-overstory habitat patches were neither preferred nor avoided relative to other cover types ($P > 0.10$).

The home ranges of radiocollared, high-elevation ecogroup deer contained cover types in similar proportion to their availability in background habitat mosaics ($T_2 = 0.42$, $P > 0.50$) (Table 4). Likewise, use of cover type patches was relatively proportional to their availability in high elevation deer summer home ranges ($T_2 = 1.68$, $P > 0.25$) (Table 4).

TABLE 3. Results of summer cover-type use analyses based upon ranks of differences between use and availability (Friedman 1937) for mid-elevation ecogroup, radiocollared Klickitat Basin black-tailed deer summering on corporate timberlands (n = number of radioed deer in analysis).

Cover Type[a]	Mean Availability	Ranks Sums (U-A)[b]	Preference Rank[c]
Landscape Scale (n=10)			
Open / shrub	0.04	33.0	4[d,e]
Open conifer	0.33	21.0	2[d,f]
Closed conifer	0.07	28.0	3[g]
Mature / Old growth	0.56	18.0	1[e,f,g]
Patch (n=15)			
Open / shrub	0.04	38.5	3
Open conifer	0.38	28.0	1[d]
Closed conifer	0.06	44.5	4[d,e]
Mature / Old growth	0.52	29.0	2[e]

[a]Open / shrub = non-forested; open conifer = < 40% canopy closure (CC); closed conifer = ≥ 40% CC, < 9 in. dbh; mature / old growth = ≥ 40% CC, > 9 in. dbh.
[b]Sum of ranks of differences in use and availability percentages for all radiocollared deer.
[c]Overall rank of preference [1 = most preferred] [ranks denoted by shared superscript are significantly different, $P < 0.10$].

TABLE 4. Results of summer cover-type use analyses based upon ranks of differences between use and availability (Friedman 1937) for high-elevation ecogroup, radiocollared Klickitat Basin black-tailed deer (n=8).

Cover Type[a]	Mean Availability	Ranks Sums (U-A)[b]	Preference Rank[c]
Landscape Scale			
Open / shrub	0.16	19.0	2
Open conifer	0.21	22.0	3.5
Closed conifer	0.20	17.0	1
Mature / Old growth	0.43	22.0	3.5
Patch scale			
Open / shrub	0.14	23.0	3
Open conifer	0.20	24.0	4
Closed conifer	0.19	14.0	1
Mature / Old growth	0.47	19.0	2

[a] Open / shrub = non-forested; open conifer = ≤ 39% canopy closure (CC); closed conifer = ≥ 40% CC, < 9 in. dbh; mature / old growth = ≥ 40% CC, > 9 in. dbh.
[b] Sum of ranks of differences in use and availability percentages for all radiocollared deer.
[c] Overall rank of preference [1 = most preferred] [ranks denoted by shared superscript are significantly different, $P < 0.10$].

Discussion

Analytic Approach

I used seasonal home ranges, estimated from telemetry, to define sampling frames for landscape and patch scale habitat selection questions. Home range estimation has been discussed extensively in the literature (Van Winkle 1975, Samuel et al. 1985, Worton 1987, 1989). It is known that estimates of home range size are affected by model assumptions, treatment of outliers, and sample sizes (Van Winkle 1975, Worton 1987, Seamon and Powell 1996). Obviously other methods would have yielded somewhat different estimates of home range size and shape. Although MCP home range estimates are sensitive to outliers, they require few distributional assumptions (Ackerman et al. 1989). Likewise, many probabilistic models perform poorly unless sample sizes are larger than those used to estimate seasonal use areas of deer in this study (Worton 1989). Given the trade-offs between home range models, sample-size constraints, and the need to simply identify an objectively-determined sampling frame for habitat questions I had framed, I believe my use of MCP estimates was a reasonable approach.

Rank testing methods for studying animal preference for habitats have many desirable features (Alldredge and Ratti 1986). However, reducing data to ranks reduces the resolution of some information available regarding animal use. These methods also may obscure distinctive patterns of certain individual animals. It was apparent in this study that some deer had home ranges centered on specific habitat features such as a clearcut, a shrub-field, or a riparian zone that did not always emerge as important population-level habitat features. The methods of Friedman (1937) and Johnson (1980) are clearly designed to yield inference that is weighted towards common patterns among all animals as opposed to individuals. Although it is interesting to note prominent individual patterns, managers should emphasize the maintenance of habitat conditions that are predictably used by most individuals. Thus, I recognize that the analytical approach I employed may have obscured some habitat selection behaviors. However, I believe the methods were appropriate for yielding insight into important population-level patterns.

The rank testing methods I employed also produced a ranking of habitats from least to most

preferred, even when differences between the rankings were not statistically significant. Although trends may be suggested in some non-significant relationships, I attempted to clearly flag those rank differences that were significant and emphasize significant relationships in the results and following discussion.

Winter Habitat Relationships

In contrast with the background habitat mosaic during winter, radiocollared deer appeared to select home ranges with more nonforested, oak, and oak/pine fringe habitat. These cover types are generally associated with lower elevation, xeric environmental settings in the KRB. Deer also selected winter home ranges with less mixed conifer habitat than was locally available. Within the general vicinity of the winter trapping area, extensive mixed conifer cover was typically associated with higher elevation uplands and cold air sinks. Winter deer home ranges were, therefore, associated with cover types that predictably received less snow, more radiant energy, and had more open canopies. In such settings, deer would find energetically less demanding winter habitat and more accessible forage. Acorns, a source of energy and nutrients during critical winter months, were also relatively easily obtained beneath oak canopies.

Within winter home ranges, radiocollared deer also demonstrated selection for oak, oak/pine, and mixed conifer patches relative to nonforested components. Although home ranges contained less mixed conifer habitat than the background mosaic, radiocollared deer appeared to selectively use mixed conifer patches within their winter home ranges. As previously noted, it seems likely that the bulk of the mixed conifer cover type in the vicinity of the winter concentration area was associated with unfavorable wintering macrohabitat; however, when conifer stands did occur close to more preferred macrohabitats such as extensive oak and oak/pine habitat, deer readily used mixed conifer stands for cover.

During winter, oak-dominated habitat patches appeared to provide preferred foraging settings for deer. Forage within oak-dominated habitats included acorns and sub-shrubs; during the severe winter of 1992-93, deer were also noted foraging extensively on arboreal lichens that were common in oak stands. High trapping success in oak-dominated stands relative to other cover types also suggested habitats with a strong oak component were preferred by wintering deer.

Suring and Vohs (1979) found that Columbian white-tailed deer (*O. virginianus leucurus*) preferred habitat components providing substantial cover and forage over components providing either alone. Likewise, this intuitive preference of deer for habitat structure meeting multiple ecological needs was suggested by Loft and Menke (1984) for wintering black-tailed deer in northern California. Coniferous forest ecotone habitat in the KRB (i.e., oak and oak/pine habitat) probably provided both quality forage and cover relative to open habitat components and extensive closed-canopy mixed conifer stands, which provided either primarily forage or cover alone.

Summer Habitat Relationships

Mid-elevation, summer deer habitat on the Yakama Reservation is managed primarily using uneven-aged silviculture, whereas on corporate timberlands in the KRB, a mix of even-aged and uneven-aged management has historically been used. This difference in management has led to substantial differences in the structure of post-logging conifer stands. GIS analyses indicated that deer summering on tribal land had a greater area of mature and old-growth and small-diameter, closed-canopy conifer habitat available in both background and home range habitat mosaics relative to deer summering on private land. Open-canopy conifer habitat and clearcuts were more abundant on managed private lands than on tribal lands.

Mid-elevation deer summering on tribally managed lands used non-forested and open-canopy conifer habitat less than expected in the absence of selection at the home range and habitat patch scale. On an uneven-aged, managed landscape, such habitats were typically associated with xeric site conditions or stands that were harvested heavily during previous entries. Although open-canopy habitat is often generalized as being forage-producing habitat with considerable value to wild ungulates, radiocollared, mid-elevation, reservation deer displayed little selection for open-canopy or nonforested habitat. Although black-tailed deer have been generalized as an ecotone species (Witmer et al. 1985), empirical data have been variously supportive of (Hanley 1983) and

contrary to (Kirchhoff et al. 1983) this hypothesis, depending on climatic and other environmental features of study areas. In my study, the use of aerial diurnal point locations may have undersampled deer involved in major crepuscular foraging bouts. However, my approach of using a 3.14 ha habitat use plot centered on the point relocations did not detect any widespread affinity for openings or open-canopy stands among radiocollared deer. It is likely, however, that smaller openings were inadequately mapped, and GIS-based analyses may have subsequently underestimated use of these smaller openings by radiocollared deer.

Radiocollared deer preferentially used mature and old-growth habitat at a landscape scale regardless of whether they summered on reservation or corporate timberlands. On corporate land, mature/old-growth was ranked as the second most-preferred habitat at a patch scale, although it was significantly preferred only over young, closed-canopy stands. Mature and old-growth forest habitat has been shown to provide preferred summer habitat for black-tailed deer, despite the generalization that mature, closed-canopy forests provide little ungulate forage (Kirchhoff et al. 1983, Loft et al. 1984, Hanley et al. 1989). Parker and Robbins (1984) experimentally determined an upper critical environmental temperature of 25 C° for summering mule deer. Older, closed-canopy forest stands in the Klickitat may have provided an energetically favorable thermal environment for summering deer during the warm, dry summers characteristic of the eastern slopes of the Cascade Range.

Apparent preference for open-canopy conifer stands on corporate timberlands attests to the adaptability of black-tailed deer, a generalist herbivore. During this study, logging occurred in the home ranges of a few radiocollared deer, and previously logged habitat occurred in several deer home ranges. In general, active logging temporarily displaced deer to parts of their home range beyond the logging disturbance. To my knowledge, no deer abandoned a home range already documented by radiotelemetry because of logging. Because home range fidelity was strong, it appeared deer coped with habitat change mediated by logging.

Site fidelity among deer, especially females, complicates the interpretation of management-induced change on habitat quality. For example, it is difficult to determine whether a deer with logged habitat in their home range selected the home range because of, or in spite of, management-induced features, because their fidelity to a female home range tradition is so strong (McCorquodale, *in press*). Deer with home ranges perturbed by management may have had matrilineal fidelity to the site before the habitat alteration. Ultimately, habitat value should be defined not simply by preference behavior, but by the influence of habitat on individual fitness. Longer term data on survival and reproductive success for deer with known home range traditions and experimentally-controlled habitat change would be required to rigorously test hypotheses of this nature. Neither this nor any previously published study has yielded such hypothesis testing.

Management Implications

The seasonal habitat mosaic for KRB deer includes limited public land, unlike the scenario for many western big game populations. During summer, KRB deer primarily depend on habitat provided by the Yakama Indian Reservation and corporate timberlands. Winter range, a limiting factor for many western big game populations, is predominantly provided by state and private land in the KRB.

Because Klickitat deer, a resource owned collectively by both the tribal and nontribal public, depend heavily on privately-owned and managed land, long-term habitat conservation is an important concern for managers. Historically, managers of public wildlife resources have had greater control over habitat management on public lands than on private lands. Likewise, federal environmental laws applicable to federal public lands often have more limited applicability on private lands.

In the last several decades, considerable low elevation deer habitat has been converted to agricultural and rural development. During this study, new home building continued within the winter study area. Continued habitat conversion or development in the lower KRB can only further reduce the winter carrying capacity of this area and increase the relative impact of periodically severe winters on deer survival (McCorquodale, *in press*). Similarly, decades of fire suppression in the lower Klickitat has led to encroachment of

ponderosa pine into areas once dominated by nearly pure oak stands. Winter habitat maintenance and enhancement should remain a high priority for Klickitat deer managers. Given the importance of privately-owned deer winter range, cooperative agreements providing an incentive for large landowners to conserve winter deer habitat values may be required to achieve long-term habitat conservation objectives.

Habitat use by Klickitat deer suggested considerable affinity for older forest stands on summer range. Thus, retention of some older, mid-elevation forest stands across the landscape in the more xeric portions of black-tailed deer range should also be a management priority. Winter habitats with a strong oak component appeared to have substantial value to deer in this region as evidenced by predictable preference among a large sample of radiocollared deer. Oak/pine ecotone habitats may require manipulations such as prescribed fire to maintain a strong oak component in the face of natural succession.

Acknowledgements

I thank G. Rankel, R. Sampsel, and W. P. Bradley for help in obtaining funding for this study. P. Aleck, C. J. Meninick, and M. Pachpe provided administrative support. Yakama Nation Wildlife Technicians J. Carl, N. Hill and V. Smartlowit assisted with all aspects of the field work. Pilots T. Byrne, C. Hilmes, and the late R. Gilkerson skillfully flew aircraft used to track radiocollared deer. The Washington Department of Fish and Wildlife (WDFW) provided access to state lands for deer trapping. I thank D. Morrison of the WDFW for his considerable help in the field and for enthusiastically supporting the project. Boise Cascade Corporation and Champion International Corporation provided access to their lands and also provided GIS data.

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Received 13 October 1998
Accepted for Publication 7 March 1999

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Vegetational Heterogeneity along Elevational Gradients

Abstract

How vegetation recovers from disturbance is a central ecological question. We tested the hypothesis that plant spatial heterogeneity declines with increasing functional vegetation age. As pioneers expand and more species invade, we expect heterogeneity to decline. Biomass accumulation and seedling recruitment both drive succession and proceed more slowly at higher elevation. Therefore, we predicted that higher elevation sites would be more heterogeneous than lower sites. We sampled vegetation in five habitats on Mount St. Helens to study recovery 17 years after its most recent eruption. Two lahars were undergoing primary succession and one ridge was recovering from nearly total destruction. A second ridge had been greatly impacted by the blast, while a fifth site was little damaged. Plant cover was analyzed using percentage similarity (PS) and detrended correspondence analysis (DCA). PS decreased with elevation on lahars and on the devastated ridge, but no clear trend was found on less impacted sites. The variation in DCA scores of samples at a site suggested increasing heterogeneity with elevation on one lahar and the strongly disturbed secondary site. The other transects did not show this pattern. These patterns support the hypothesis that heterogeneity declines with increasing successional age. Implicit in the hypothesis is that stochastic factors are important to the establishment of vegetation. High variability among samples of stable vegetation at lower elevation sites suggests that the effects of stochastic establishment can persist.

Introduction

Species assembly during early primary succession is not well understood. Here we compare spatial heterogeneity of vegetation at sites recovering from volcanic impacts on Mount St. Helens. Studies of this volcano suggested that stochastic dispersal (del Moral et al. 1995, del Moral 1998, 1999, Tu et al. 1998) and few safe sites (Tsuyuzaki et al. 1997, del Moral and Grishin 1999) produce initially heterogeneous vegetation. We used a variant of a space-for-time substitution approach to test the hypothesis that spatial heterogeneity declines over time.

The 1980 eruption of Mount St. Helens dramatically altered the surrounding landscape to create a mosaic of impacts (Halpern et al. 1990). A map of impact types appears in del Moral and Bliss (1993). This study describes succession on lahars (mud flows) and recovery on ridges affected to varying degrees. We investigated the hypothesis that vegetation heterogeneity increases with elevation. We assume that an elevation gradient can simulate a temporal gradient. This assumption is based on the fact that high-elevation sites have an effectively shorter history than those at lower elevations because shorter growing seasons and slowed physical amelioration (del Moral and Wood 1993) reduce plant growth and seedling recruitment (Titus and del Moral 1998). Therefore, if stochastic factors dominate early vegetation establishment, then recovering vegetation should be more variable at higher sites than at lower ones.

Materials and Methods

Mount St. Helens (46° 12' N, 112° 11' W) erupted on May 18, 1980. The heat of the eruption melted snow on the cone's east, south, and west sides to spawn lahars that filled valleys and scoured ridges (Foxworthy and Hill 1982). In 1996, 17 growing seasons after the eruption, we sampled vegetation on 1) lahars that are undergoing primary succession, 2) a scoured ridge and a blasted ridge that are experiencing secondary succession (after a partial loss of species), and 3) sites that have fully recovered from minor impacts (cf., Grishin et al. 1996). These sites offered an opportunity to explore how heterogeneity changes during succession.

We studied five transects: Fire Creek, Muddy River, Pine Creek Ridge, Toutle Ridge and Butte Camp. The Fire Creek (900 to 1115 m) and Muddy

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River (790 to 1140 m) transects sampled lahars on the east flank of the cone. Both are primary substrates with little organic matter. Surface heterogeneity at each site was similar, and there were no discernible differences in the type or frequency of microsites. The Fire Creek transect was downwind from and near intact vegetation, while the Muddy River transect was upwind and more distant from vegetation (Halpern and Harmon 1983, del Moral 1993). The Pine Creek Ridge (1340 to 1615 m) transect was along a ridge that had been scoured by lahars. Most soil had been removed, but some plants survived (del Moral 1981, 1983; del Moral and Wood 1988). Permanent plots documented that recovery has been gradual and related to elevation. Each sample was on sloping terrain that lacked significant major microsite features. Surface heterogeneity was similar throughout the transect, though the lower clusters had suffered less erosion. Toutle Ridge (1370 to 1615 m) is on the west side of the cone on the edge of the lateral blast. Although trees were killed and some soil was removed, there was substantial survival (del Moral and Wood 1988). High elevation sites were more intensely impacted than lower elevation ones, but surface heterogeneity was similar throughout the transect. Butte Camp (1385 to 1720 m) included three transects on the southwest side of the volcano. These sites experienced only a modest deposit of sandy pumice.

This study was designed to determine the hierarchical nature of spatial heterogeneity. The basic sampling unit was a 1 m^2 *quadrat* within which percent cover was estimated to the nearest 1%. Ten quadrats sampled a circular *plot* with a 10 m radius (314 m^2). Species not sampled, but present, were given cover values of 0.05%. Species within 10 m of the plot, but not in the plot, were given a value of 0.005%. Five plots described a *cluster* and several clusters constituted a *transect*. A transect was started at the center of a plot in representative vegetation while avoiding secondary disturbances such as drainages. The 10 1-m^2 quadrats were placed at 2 and 5 m from the center on the cardinal directions and at 2 m on two additional radii. The four additional plots of a cluster were located 10 to 30 m (randomly determined) in each of the cardinal directions from the center plot.

Heterogeneity was quantified using percentage similarity of cover data (PS) among each sample pair at each level in the hierarchy (among quadrats, among plots and among clusters). PS was calculated using MVSP (Kovach 1993):

$$PS_{ij} = \frac{200\ \Sigma_k\ min\ (X_{ik}, X_{jk})}{\Sigma_{\underline{k}}(X_{ik}+X_{jk})}$$

where $\underline{k}$ = the total number of species, X_{ik}, and X_{jk} = the cover of species $\underline{k}$ in each of two samples, $\underline{i}$ and $\underline{j}$, and $\underline{min}$ is the minimum value. Faith et al. (1987) suggested that percentage similarity was a useful measure of species composition. High similarity implies homogeneous samples, while low similarity implies heterogeneity. Spearman rank order correlations (r_s) and linear regressions (r_l) between elevation and similarities were calculated (Analytical Software 1994).

Detrended correspondence analysis (DCA; Hill and Gauch 1980; McCune and Mefford 1997) was used to provide a description of the transects and to assess within-cluster variation. Rare species (frequency < 20% of the most common frequency) were reduced in importance in proportion to their frequency (downweighting). Species that occurred only once were omitted. The arch common to other eigen analyses was eliminated by dividing the first axis into 26 segments and setting the average score on the second axis to zero within each segment. The dispersion of plots within a cluster was determined by the standard deviation of the first DCA axis score along each transect. Each analysis provided an eigenvalue, percent variation on each axis and gradient lengths for comparison.

Results

Sixty-seven species, including conifers, shrubs, forbs, graminoids and mosses, were encountered. There were nearly equal numbers of species at each site: Muddy River, 38 species; Fire Creek, 40 species; Pine Creek, 35 species; Toutle Ridge, 37 species; and Butte Camp, 38 species. Twelve species occurred at every site. Table 1 shows overall cover changes at each site.

The vegetation of the two lahars differed considerably, though both were dominated by rock moss (*Racomitrium canescens*). There were no consistent vegetation patterns at Fire Creek. Cardwell's penstemon (*Penstemon cardwellii*) dominated the middle of the transect, but other species were sporadic. On the Muddy River, dominance shifted from prairie lupine (*Lupinus lepidus*)

TABLE 1. Mean total cover percent of clusters along each transect. Elevations are relative to each transect, starting point adjusted for starting elevation.

	Transect				
Elevation	Muddy River	Fire Creek	Pine Creek Ridge	Toutle Ridge	Butte Camp
Low	111	86			
	75	40			
	48	43			
	16	23	74	41	
	14		77	38	55
Moderate	19		33		49
			31	17	
			20	31	36
			14		17
High			2	8	16

at lower elevations to Cardwell's penstemon and pearly everlasting (*Anaphalis margaritacea*) at higher elevations. Cascade lupine (*L. latifolius*) and subalpine fir (*Abies lasiocarpa*) were dominant at the highest site.

Plant cover at Pine Creek Ridge declined with elevation. Thin bentgrass (*Agrostis diegoensis*) dominated throughout, though its cover was reduced at higher elevations. At lower elevations, several species, including prairie lupine, Cascade lupine, Parry's rush (*Juncus parryi*), Cascade aster (*Aster ledophyllus*) and rock moss, were common. Cover of alpine buckwheat (*Eriogonum pyrolifolium*) and Cardwell's penstemon peaked at mid-elevation.

Toutle Ridge was well vegetated, though cover decreased with elevation. Low elevation plots were dominated by thin bentgrass, Cascade lupine, Cardwell's penstemon, yarrow (*Achillea millefolium*), and rock moss. At mid-and upper-elevations, prairie lupine replaced Cascade lupine, Martindale's lomatium (*Lomatium martindalei*) were common while mosses declined.

Cover declined slightly with elevation at the Butte Camp sites. Grasses declined substantially, but common species such as fleeceflower (*Polygonum newberryi*), alpine buckwheat, and Cardwell's penstemon off-set this reduction with large increases.

Percentage Similarity (PS)

The Muddy River transect spanned 340 m (800 m to 1140 m). The mean PS among the 10 quadrats of a plot declined with increasing elevation from 81.8 to 31.8%. The linear regression was r_l = -0.97 ($P < 0.001$), while the Spearman rank correlation (r_s) was -1.00 ($P < 0.03$; Figure 1). The mean similarities of plots within a cluster were higher, but also declined with elevation from 84.5% to 63.5% (r_l = -0.62, $P < 0.001$; r_s = -0.83 ($P < 0.06$). The overall mean similarity of the six clusters was low 36.5 (8 to 78%), indicating that there was significant variation along this short coenocline.

The Fire Creek transect spanned 210 m (900 to 1110 m). The mean PS of quadrats within a plot declined with increasing elevation from 78.6 to 44.8% (r_l = -0.81, $P < 0.001$; r_s = -1.00, $P < 0.09$; Figure 2). Cluster mean PS declined with increasing elevation from 83.3 to 58.8% (r_l = -0.80, $P < 0.001$; r_s = -1.00, $P < 0.09$). The mean similarity between clusters was 56.1 (18 to 86%),

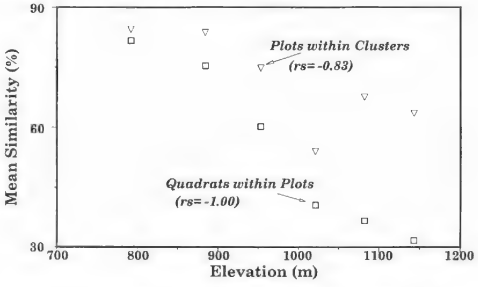

Figure 1. Mean percent similarity of quadrats within plots and plots within clusters on the Muddy River transect. The Spearman's rank order test (r_s) of quadrats in plots vs. elevation was $P < 0.03$; r_s of plots in clusters was significant ($P < 0.06$).

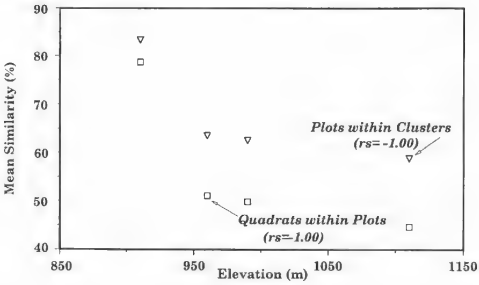

Figure 2. Mean percent similarity of quadrats within plots and plots within clusters on the Fire Creek transect. The Spearman's rank order test (r_s) of quadrats in plots vs. elevation was $P < 0.09$; r_s of plots in clusters was $P < 0.09$).

reflecting greater dominance by mosses and proximity to intact vegetation.

The Pine Creek transect spanned 280 m (1340 and 1620 m). The mean PS of quadrats within a plot declined with elevation from 67.2 to 33.1% (r_l = -0.67, P < 0.001; r_s = -0.71, P < 0.08; Figure 3). Cluster mean PS declined with increasing elevation from 79.4 to 48.9% (r_l = -0.79 (P < 0.001; r_s = -0.78 (P < 0.06). The mean between cluster similarity was 35.8% (1 to 82%) reflecting the steep coenocline and isolation of each cluster.

The Toutle Ridge transect spanned 245 m (1370 to 1615 m). The mean PS of quadrats within a plot varied from 38.6 to 54.8% (Figure 4), with no significant trend (r_l = -0.12, n.s.; r_s = -0.3, P < 0.54). The similarity between plots of a cluster ranged from 51.9 to 73.2%, with no significant elevational trend (r_l = +0.04, n.s.; r_s = 0.40, P < 0.42). The PS between clusters was 38.3 (16 to 59%) indicating that there was significant vegetation change along the coenocline, but that it was not necessarily correlated to elevation.

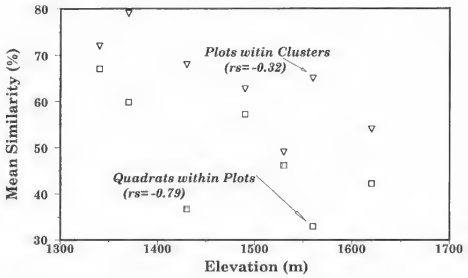

Figure 3. Mean percent similarity of quadrats within plots and plots within clusters on the Pine Creek transect. The Spearman's rank order test (r_s) of quadrats in plots vs. elevation was P < 0.08; r_s of plots in clusters was P < 0.06).

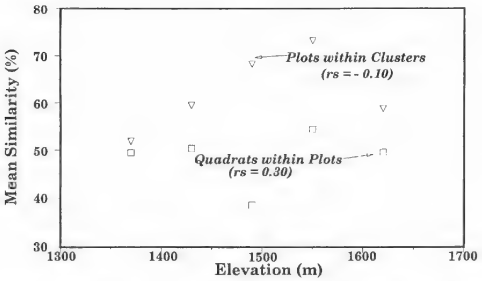

Figure 4. Mean percent similarity of quadrats within plots and plots within clusters on the Toutle Ridge transect. The Spearman's rank order test (r_s) of quadrats in plots vs. elevation was P < 0.30; r_s of plots in clusters was P < 0.42).

The three Butte Camp transects ranged over 200 m (1520 to 1720 m). Mean PS between quadrats of a plot varied from 39.7 to 58.6%, with no significant correlations with elevation. Variation in mean similarity of plots within a cluster varied from 36.2% to 67.6%, with no significant correlations. Mean similarity between clusters was 33.6% (18 to 57%), comparable to other sites. If data from the three transects were combined, there was a significant linear correlation between elevation and within-cluster similarity (r_l = -0.69, P < 0.05). There was no within plot variation trend with elevation in the combined data at Butte Camp.

Detrended Correspondence Analysis (DCA)

DCA provided an alternative way to assess within-cluster variation. Each transect was analyzed independently to determine any significant differences in the structure of the data (Table 2). There were no striking structural differences, but inertia (variance) increased with successional age. Primary surfaces and Pine Creek had low inertia due to strong dominance and low within cluster diversity. The Toutle Ridge and Butte Camp transects had high inertia due to reduced dominance and high within cluster richness. The gradient lengths reflected these differences. The fraction of the explained variance on Axis I was lower for Butte Camp than the primary surfaces because there was greater species richness and equitability at Butte Camp.

TABLE 2. Eigenstructure for each transect analyzed separately.

	Transect				
Parameter	Muddy	Fire	Pine	Toutle	Butte
Eigenvalue I	0.55	0.69	0.48	0.56	0.59
Eigenvalue II	0.22	0.20	0.11	0.30	0.34
Total inertia	1.80	1.60	1.66	2.17	3.62
Gradient Length I	2.69	3.45	3.83	3.19	4.02
Gradient Length II	2.08	1.03	1.70	2.16	2.66
Explained Variance I	30.8	43.5	29.2	25.9	16.4
Explained Variance II	12.2	12.4	6.4	13.6	9.9

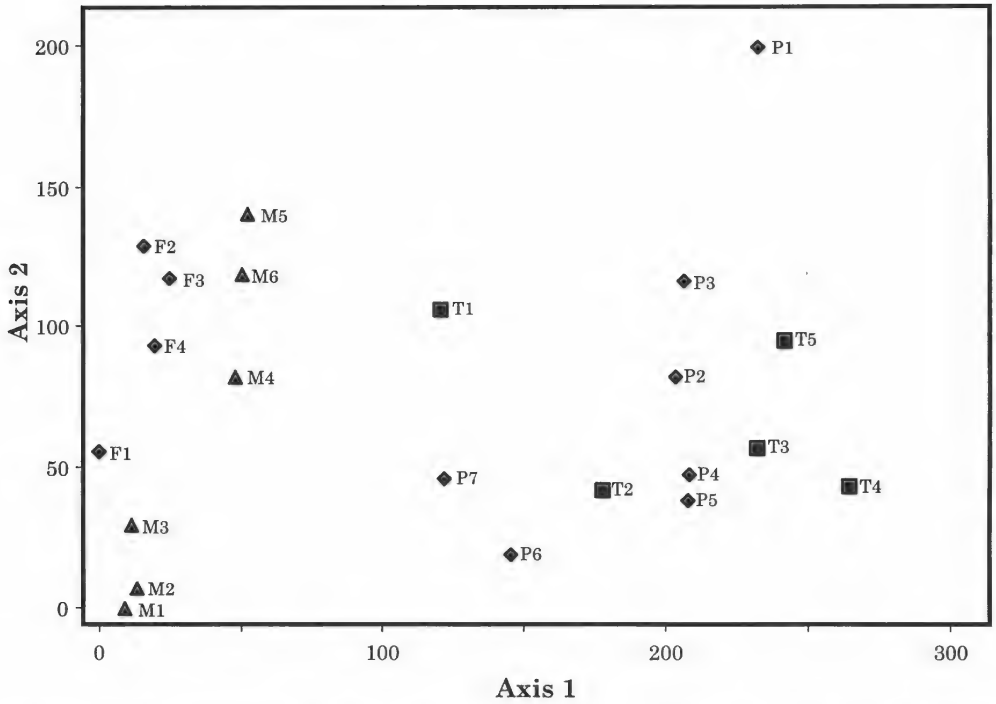

Figure 5. Detrended correspondence analysis of primary successional lahars (M = Muddy River; F = Fire Creek) and a scoured secondary successional ridge (P = Pine Creek Ridge) and a blasted secondary successional ridge (T = Toutle Ridge). Numbers indicate cluster number and increase from low to high elevation for each transect.

Mean cover in each plot of the four successional transects was analyzed to determine transect variation (Figure 5). The lahars (FC and MR) had low Axis I scores, while the secondary sites (TR and PC) had high Axis I scores. Spearman rank correlations (r_s) between elevation and axis scores were determined. The elevation of Muddy River plots increased significantly with both Axis I ($r_s = 0.89$, $P < 0.05$) and Axis II ($r_s = 0.94$, $P < 0.04$). The correlation between Fire Creek elevation and Axis I not significant ($r_s = 0.80$, $P < 0.16$) due to low sample size. The elevation of Pine Creek Ridge plots decreased along Axis I ($r_s = -0.68$, $P < 0.1$) and more strongly along Axis II ($r_s = -0.86$, $P < 0.04$). Toutle Ridge elevation increased along Axis I ($r_s = 0.90$, $P < 0.08$).

A weak pattern of among cluster variation (measured by the standard deviation of Axis I scores) emerged when each transect was analyzed independently (Table 3). There was no trend in the DCA variation on the Muddy River transect.

TABLE 3. Standard deviations of first axis DCA scores of plots within clusters. Each transect was analyzed independently. Elevations are relative to transect.

Elevation	Transects			
	Muddy River	Fire Creek	Pine Creek Ridge	Toutle Ridge
Low	.285	.074		
	.250	.119		
	.092	.040		
	.472	.384	.130	.309
	.145		.152	.509
Moderate	.267		.227	
			.296	.193
			.324	.214
			.279	
High			.318	.472

This may be because this transect was isolated from donor populations and spans a moderate elevation. There was a trend of increased heterogeneity along the elevational gradient on the Fire

TABLE 4. Percent similarity at three scales in four transects. Asterisks indicate significant changes with elevation.

Transect	Elevation Range (m)	Quadrats in Plots	Plots in Clusters	Clusters
Muddy	340	81.8 to 31.8%*	84.5% to 63.5%*	36.5
Fire Creek	210	74.8 to 50.1*	83.3 to 58.8	56.1
Pine Creek	280	67.2 to 33.1*	79.4 to 48.9%*	35.8
Toutle	245	38.6 to 54.8	51.9 to 73.2	38.3

Creek transect. The three lower clusters were near existing vegetation and had received similar influxes of vegetation. The upper site was variable and was the most isolated of the clusters. The Pine Creek Ridge transect showed a trend of increasing heterogeneity with elevation. Though the lowest Pine Creek sites were at higher elevations than the Fire Creek clusters, they were more homogeneous, presumably because they retained a significant residual vegetation. The within-cluster DCA variation on Toutle Ridge was inconsistent, though variation was greater than that of Pine Creek Ridge. Butte Camp variability was high in most cases, but with no apparent trend.

Discussion

Heterogeneity increased with elevation on both lahars and Pine Creek Ridge. Since elevation is related to effective successional time, this result supports the hypothesis that heterogeneity declines during succession. Mean PS declined with elevation among quadrats in a plot and among plots in a cluster. In contrast, we observed no trends at Toutle Ridge or Butte Camp. At these sites, soil and a seed bank survived the eruption and recovery was dominated by residual species that were already well distributed.

A different similarity pattern emerged for vegetation on each transect (Table 4). Within plot similarity has the greatest range on the Muddy River transect, the most isolated transect. Plots within a cluster were relatively homogeneous, due low richness and strong dominance, but clusters differed strongly from one another, in part due to the range of the gradient and in part due to the stochastic nature of invasion patterns. The upper end of this transect was in an early assembly mode while the lower end had begun to fill in gaps by secondary dispersal. The result was that the vegetation of the lower portion was more homogeneous than the upper portion. Lahars on the south side of Mount St. Helens have undergone similar homogenization (del Moral 1998). At Fire Creek, the small elevational range of the transect and its proximity to intact vegetation limited PS changes and resulted in the highest degree of similarity among the clusters. However, heterogeneity did increase significantly with elevation. Pine Creek is developing as if it were a primary successional site. Only a few individuals survived and development has required dispersal from below. Observations made since 1980 suggest that most species have advanced gradually uphill by short distance dispersal. Thus, there is a decline in similarity with elevation at both scales, and between cluster similarity is the least of the four transects. Toutle Ridge had significant surviving vegetation. Despite considerable recovery and colonization since the eruption, there were no trends in similarity over the elevation range sampled. Similarity patterns were not found at Butte Camp.

An alternative method to investigate variation produced ambiguous results. Variation in DCA I scores on the Muddy River was inconsistent. The low PS at Cluster 4 corresponds to the high DCA variation at this site, but otherwise there were few points of congruence. In contrast, at Fire Creek and Pine Creek, there were consistent increases in within-cluster variation with elevation that mirrored the patterns exhibited by PS data. DCA also did not demonstrate a trend on Toutle Ridge. DCA demonstrated progressive changes among plots on each transect. Such trends are usually interpreted as the results of elevation. Here, we suggest that different relative successional stages could contribute to the observed regularities in DCA scores.

The large between cluster heterogeneity on the Toutle transect and at Butte Camp suggests that stochastic factors may not dominate only early in primary succession and then disappear due to deterministic factors such as competition. Chance may control patterns along a continuous gradient that parallel patterns caused by disturbance.

Stochastic factors appear to be a strong force in primary successional sites, but those factors are masked when species survive in more moderately impacted sites. Elements of stochastic initiation of vegetation may never be obliterated and must be considered in the analysis of vegetation pattern (Lavorel and Lebreton 1992, del Moral et al. 1995). Though certain life-history traits may be favored on particular substrates (Tsuyuzaki and del Moral 1995), species composition is affected by landscape factors that produce initially heterogeneous vegetation.

In this study we demonstrated that less mature vegetation was more variable than more mature vegetation. We used elevation as a surrogate for relative successional time. As habitat variability did not change perceptibly along any transect, we are confident that factors related to elevation, not habitat heterogeneity, are responsible for the observed vegetation responses. Similar trends of declining heterogeneity should be expected in long-term chronosequence studies and in the comparison of sites at which other factors contribute to a gradient of different effective developmental age.

Acknowledgements

Financial assistance was provided by National Science Foundation Grant No. DEB 94-06987 and by a N.S.F. REU grant. We thank S. Bard for her fine field assistance and N. Wolf for editorial comments. Mount St. Helens National Volcanic Monument granted permission for this study.

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Received 12 December 1997
Accepted for Publication 14 January 1999

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Use of Woody Debris Piles by Birds and Small Mammals in a Riparian Corridor

Abstract

Woody debris piles, a natural component of rivers draining the coastal forests of the Pacific Northwest, provide a unique resource in the riparian-river corridor. We describe the distribution of woody debris piles on the Skykomish River, Washington, and examine their use by birds and small mammals. We found an average of one debris pile per 15 m of river bank; the inside of these piles was significantly cooler than the ambient environment. Over sixteen bird species were observed using the debris piles while other bird species in the area were never observed on the debris piles. The overall species richness of small mammals was greater at debris piles (9 species) than at reference sites in nearby areas without woody debris (4 species). On cobble bars, there was a greater abundance of small mammals at debris piles than at reference sites. We conclude that debris piles may provide valuable resources to both birds and small mammals particularly on otherwise barren cobble bars.

Introduction

Rivers in the coastal forests of the Pacific Northwest region of North America transport considerable woody debris as logs, branches, and rootwads. During high flows, woody debris accumulates on gravel bars, on channel shores, in riparian forests, and even in upland forests where the channel has migrated suddenly (Bilby and Bisson 1998). Historically, debris has been an integral component of Pacific Northwest stream ecosystems (Gurnell et al. 1995). Archival records document streams that were filled with fallen trees and major river systems choked by driftwood dams (Harmon et al. 1986, Sedell et al. 1988). Debris deposition and accumulation continue to be fundamental processes in river ecosystems (Abbe et al. 1996, Bilby and Bisson 1998, Fetherston et al. 1995). Accumulations of woody debris provide potentially valuable resources for birds and small mammals in the riparian-river corridor.

Riparian areas are biologically diverse and support extensive bird and small mammal communities (Kelsey and West 1998, Lock and Naiman 1998, Raedeke 1988, Naiman and Dæcamps 1997). Although there is a vast literature describing the dependence of many species of birds and small mammals on downed wood in upland forests (Harmon et al. 1986, Maser and Sedell 1994), and the importance of coarse woody debris to streams and aquatic organisms (Bilby and Bisson 1998, Bisson et al. 1987, Harmon et al. 1986, Maser and Sedell 1994), the value of riverine wood as habitat for terrestrial organisms has been examined only once (Mason and Koon 1985). In the riparian-river corridor, woody debris piles may aggregate scarce food resources such as seeds, insects, and fungi and also provide shelter from predators and extreme environmental conditions (Mason and Koon 1985).

In this study, we describe riparian debris piles and their use by birds and small mammals along the Skykomish River, Washington. We examine the distribution and abundance of debris piles and compare their internal temperature regimes with the external environment. We compare the abundance and species richness of birds and small mammals between piles of different sizes, between old and newly-deposited piles, and between piles on exposed cobble bars and piles in forested areas to identify key features contributing to observed patterns. For small mammals, it is possible to document changes in the use of debris piles over the breeding season and to test the hypothesis that debris piles provide habitat that is preferable to the surrounding environment.

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Methods

Study Area

The North Fork of the Skykomish River drains the western slope of the Cascade Mountains in the State of Washington, USA (Figure 1). The 1.6 km study area is located on the southern bank of this fourth order river, 14.4 km northeast of the town of Index. Channel slope is 1.8% with a side slope gradient ranging from 40-80%, typical for the Pacific Northwest coastal ecoregion (Naiman et al. 1992). The Pacific Northwest coastal ecoregion is characterized by high flows during the rainy season, from October to January. These flow rates can be as much as 100 times the minimum flow during the dry season, from August to September. The meandering channel often changes course from year to year as a result of these dramatic fluctuations in flow and is marked by shifting cobble bars both on shore and within the channel. Woody debris piles are present on most cobble bars, in the riparian forest, and at the edges of the upland forest.

Where the river has cut into the bank it flows next to an established forest. There are two types of established forest at the study site: (1) predominantly 60 year-old, second-growth Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) and (2) riparian forest composed predominantly of 40-year old red alder (*Alnus rubra*) and cottonwood (Populus trichocarpa) with western red cedar (*Thuja plicata*), silver fir (*Abies amabilis*), western hemlock, and bigleaf maple (*Acer macrophyllum*). Where the river is depositing material, there are newly formed cobble bars which support a young riparian for-

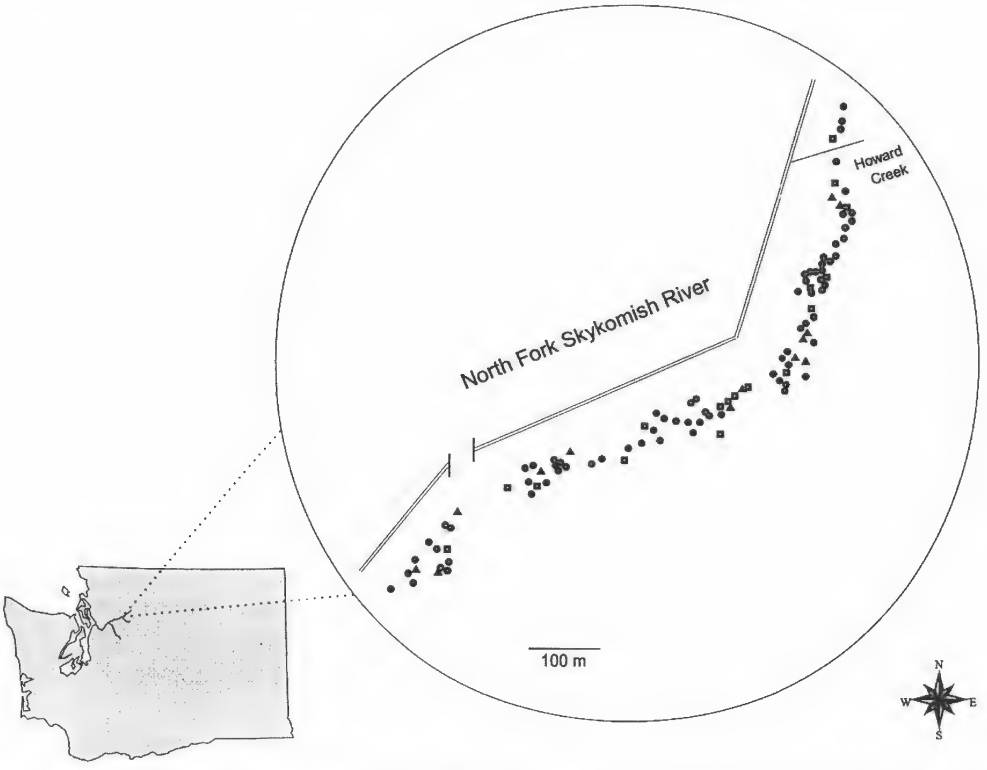

Figure 1. Study area, the North Fork Skykomish River, Washington State. Debris piles are indicated by dots. Debris piles included in the original 16-pile sample are indicated by squares. The 13 debris piles added for the final small mammal sampling are represented by triangles. The schematic includes a gap between two sampling areas, representing an unmapped 3 km portion of river.

est, composed mainly of 1 to 12 yr old red alder, willow (*Salix* sp.) and cottonwood.

In November and December, 1990, a series of three floods (approximate 40 yr recurrence interval) created new cobble bars and debris piles in the study area. We could distinguish newly deposited debris by the presence of green needles attached to the wood.

Mapping and Sampling

All debris piles were mapped and sampled between January and November, 1991. For the purpose of this study, a debris pile is defined by two criteria. It must be composed of more than one piece of river-deposited wood and it must have dimensions greater than 1 x 3 m in area. All debris piles within 50 m of the active channel were mapped over a total distance of 1609 m (Figure 1). Length, width, maximum height, age, distance to water, substrate (soil or cobble) and distance to the edge of the forest were recorded for each debris pile. Age was categorized as new (deposited in 1990) or old (deposited before 1990). Pile size was approximated by the horizontal surface area of the debris pile.

In the spring, a stratified sample of 16 piles was selected according to pile age (old or new), location (forest = soil substrate or cobble bar = cobble substrate) and size. The stratification resulted in 2 each of the 8 possible pile types, i.e. small, old, forested piles or large, new piles on cobble bars. In the fall, an additional 13 piles were similarly selected to increase the sample size for the final small mammal trapping.

Temperature Monitoring

Maximum-minimum thermometers were used to compare the thermal microclimate of the 16 original piles with ambient conditions. Thermometers, placed simultaneously inside and outside, were rotated between piles so that measurements were recorded at each debris pile for two 24-hr sampling periods in late August, early September and for two 24-hr periods in early November.

Temperature data were analyzed using paired t-tests to compare internal and external maximum and minimum daily temperatures (Zar 1984). Ecological systems are particularly variable systems; therefore, in these and subsequent statistical tests, P-values of < 0.1 were considered significant.

Avifauna

Each of the original 16 debris piles were observed for 40, 15-min observation periods between 21 June and 4 July, resulting in a total of 160 hrs of observation. Observation periods for each pile were evenly distributed from dawn until dusk. Birds were visually identified to species and their activities were recorded. Up to two activities were recorded for each bird observed on a debris pile. Bird use of debris piles was defined as landing on the pile or on an associated snag. An individual bird's location was noted as being on a perch, on the main surface of the debris pile, inside the debris pile, or on an associated snag. All birds seen or heard during the surveys but which were not using the debris piles were also identified and recorded.

Small Mammals

Spring and Fall Trapping: Two pitfall traps and two Sherman live traps were placed at each of the original 16 debris piles. The traps were set over six nights between 22-30 April and, again, over six nights between 29 August and 11 September. Sherman live traps were baited with oats and ground beef. Most animals were captured alive.

Final Trapping: Two pitfall traps, two Sherman live traps and two snap traps were placed at each of 29 debris piles, for a total of 174 traps. Traps were left open from 5-8 November. They were checked and rebaited once a day.

For the final trapping, one reference site was added for each debris pile. The reference site was an area at least 10 m from the pile and physically similar to the area of the pile but without woody debris. Similarity was based on percent forest cover, substrate, distance to the water, and overstory species composition. One pitfall trap, one Sherman live trap, and one snap trap were placed at each reference site, for a total of 87 traps.

We cut tail hairs, used eartags where possible, or removed a patch of dark outer hair to identify previously captured individuals. Mammals were identified to species in the field if captured alive or by the Burke Museum staff, University of Washington, if captured dead. Tail length was used to differentiate between deer mice (*Peromyscus*

maniculatus; ≤ 96 mm) and forest deer mice (*Peromyscus keeni*; > 96 mm) (Hogan et al. 1993). Juveniles and *Peromyscus* for whom accurate identification was not possible were classified as *Peromyscus* sp. (Gunn and Greenbaum 1986). Other common and scientific names are from Jones et al. (1992).

Data are presented as total number of individuals per species and as catch per unit effort (CPUE), the estimated capture rate for one trap per 100 trap nights. CPUE was calculated following Nelson and Clark (1973):

$$CPUE = A \times 100 / (TU - IS/2)$$

Where: A = number of animals captured, I = length of trapping interval, S = number of traps snapped, TU = P x I x N, P = number of trapping intervals, and N = number of traps. Estimates of CPUE may be conservative compared to those of other authors because we classified only those traps closed due to the capture of an animal as snapped.

We compared CPUE, and species richness between piles of different ages, sizes, and locations using Wilcoxon rank sum tests. We also used linear regression to test whether distance of a debris pile from the forest was a significant predictor of small mammal CPUE or richness. CPUE comparisons between debris piles and reference sites used permutation tests for the mean of two paired samples (Good 1994).

Results

Pile Distribution

A total of 106 piles were mapped along the 1609 m of study area, resulting in a density of one debris pile per 15 m of riverbank (Figure 1). Debris piles covered areas ranging from 3 m^2 to 530 m^2 (μ= 26.2 m^2, σ^2= 17.5) and were clustered at the upstream end of cobble bars and within the associated riparian forest. The largest piles were on cobble bars (p=0.05) and tended to be washed up against a patch of riparian forest. In some cases, vegetation growing within and directly upstream of the oldest piles was > 30 yrs old.

Internal Pile Temperature

The average maximum daily temperature was 3.2°C cooler inside the piles than outside (p<0.001). Although the average daily minimum temperature inside the piles was 0.3°C warmer than outside, this trend was not statistically significant.

Avifauna Use Patterns

A total of 125 observations of birds using debris piles (16 species) were recorded during the study period (Table 1A). American robin was the most abundant, accounting for 43% of the observations. Swainson's thrush (11%), dark-eyed junco (9%), rough-winged swallow (6%), hairy woodpecker (5%), empidonax flycatcher (5%), and Steller's jay (4%) accounted for the majority of the other observations. Eight individuals (6%) were unidentified.

TABLE 1A: Bird species observed on a debris pile.

Common Name	Scientific Name	Feeding Guild
Swainson's Thrush	*Catharus guttatus*	OGF
Steller's Jay	*Cyanocitta stelleri*	OGF
Dark-eyed Junco	*Junco hyemalis*	OGF
White-crowned Sparrow	*Zonotrichia leucophrys*	OGF
Rough-winged Swallow	*Stelgidopteryx serripennis*	IAS/IASc
Epidonax Flycatcher	*Empidonax* sp.	IAS/IASc
Western Tanager	*Piranga ludoviciana*	IAS/IASc
Cedar Waxwing	*Bombycilla cedrorum*	IAS/IASc
Winter Wren	*Troglodytes troglodytes*	IGG
Varied Thrush	*Ixoreus naevius*	IGG
Calliope Hummingbird	*Stellula calliope*	OFHG
Rufous Hummingbird	*Selasphorus rufus*	OFHG
American Robin	*Turdus migratorius*	OLCF
Black-throated Gray Warbler	*Dendroica nigrescens*	ILCG
Hairy Woodpecker	*Picoides villosus*	IBG
Belted Kingfisher	*Ceryle alcyon*	PWP

Eleven species were seen or heard in the study area but never observed on the piles (Table 1B). These include Golden-crowned Kinglet, Yellow Warbler, Yellow-rumped Warbler, Mountain Chickadee, Vaux's Swift, Western Wood Pewee, Spotted Sandpiper, Lincoln's Sparrow, Bald Eagle, Red-tailed Hawk, and Common Merganser.

The majority of bird activities (54%) at debris piles required only the physical structure of the debris pile, for example perching or hawking. In nearly one fifth of the activities, birds were observed

TABLE 1B. Bird species heard during surveys but never observed on a debris pile

Common Name	Scientific Name	Feeding Guild
Golden-crowned Kinglet	*Regulus satrapa*	ILCG
Yellow Warbler	*Dendroica petechia*	LCG
Yellow-rumped Warbler	*Dendroica coronata*	LCG
Chickadee	*Parus gambeli*	ILCG
Vaux's Swift	*Chaetura vauxi*	IASc
Western Wood Pewee	*Contopus sordidulus*	IAS
Spotted Sandpiper	*Actitis macularia*	ISG
Lincoln's Sparrow	*Melospiza lincolnii*	OGF
Bald Eagle	*Haliaeetus leucocephalus*	CGS
Red-tailed Hawk	*Buteo jamaicensis*	CGH
Common Merganser	*Mergus merganser*	PFD

Key to guild abbreviations: CGH = carnivore, ground hawker; CGS = carnivore, ground scavenger; IAS = insectivore, air sallier; IASc = insectivore, air screener; IBG = insectivore, bark gleaner; IGG = insectivore, ground gleaner; ILCG = insectivore, lower-canopy gleaner; ISG = insectivore, shoreline gleaner; OGF = omnivore, ground forager; OFHG = omnivore, floral hover-gleaner; OLCF = omnivore, lower canopy forager; PFD = piscivore, water foot-plunger; PWP = piscivore, water-plunger (modified from De Graaf et al. 1985).

simply to perch on the highest branches. Birds were also observed eating, foraging, singing, calling, and chasing. Fifteen percent of the activities included entering inside debris piles.

Small Mammal Use Patterns

Spring and Fall Trapping

The total number of mammals caught (p=0.02) and species richness (p<0.01), at each pile, increased significantly from spring to fall (Table 2).

Final trapping

Nine small mammal species were captured in the debris piles compared to four at the reference sites (Table 3). Over all sites, species richness was significantly higher at the debris piles than at the reference sites (p=0.02). At sites on the cobble bars, there was a significantly higher CPUE for total small mammals at debris piles than at reference sites (p=0.02) (Table 4).

Comparing patterns between different types of piles, the only significant finding was between new and old debris piles. There were significantly more mammals caught at new debris piles than at old debris piles (p=0.06). This trend appears to be driven by *Peromyscus keeni* which was significantly more abundant at new than at old debris piles (p=0.07 when abundance at new versus old debris piles is compared for *P. keeni* alone). New debris piles also had a significantly higher species richness than did old debris piles (p=0.08).

TABLE 2. Small mammals captured at debris piles in the spring and fall surveys by absolute number and catch per unit effort (CPUE).

	Spring		Fall	
Species	Number	CPUE	Number	CPUE
Peromyscus maniculatus	6	3.4	12	7.6
Peromyscus keeni	13	7.3	13	8.2
Peromyscus spp.	1	1.1	3	1.9
Sorex trowbridgii	8	2.2	12	3.4
Sorex monticolus	2	0.5	6	1.7
Sorex palustris			1	0.3
Sorex spp.			3	0.9
Microtus longicaudus	1	0.6	1	0.6
Microtus oregoni			1	0.6
Microtus spp.			2	1.3
Neurotrichus gibbsii			2	0.6
Zapus trinotatus			5	3.2
Total	31	15.0	61	30.1

TABLE 3. Small mammals captured at debris piles and reference sites by absolute number and catch per unit effort (CPUE). CPUE calculated for all piles together.

	Debris Pile		Reference Site	
Species	Number	CPUE	Number	CPUE
Peromyscus maniculatus	10	2.2	5	2.2
Peromyscus keeni	6	1.3	4	1.8
Peromyscus spp.	1	0.2		
Sorex trowbridgii	6	0.9	1	0.3
Sorex monticolus	2	0.3	1	0.3
Sorex palustris	1	0.2		
Microtus longicaudus	3	0.7		
Microtus oregoni	1	0.2		
Neurotrichus gibbsii	1	0.2		
Scapanus orarius	1	0.2		
Total	32	6.3	11	4.6

TABLE 4. Mean catch per unit effort (CPUE) of small mammals by genera for debris piles and reference sites on the cobble bar and in the forest.

	Cobble Bar		Forest	
Genus	Debris Piles	Reference Sites	Debris Piles	Reference Sites
Peromyscus	8.0	3.9	4.1	9.5
Sorex	1.6	0.0	2.7	1.5
Microtus	2.7	0.0	0.0	0.0
Total	12.3	3.9	6.8	11.0

Size was not a significant indicator of debris pile habitat value. The smallest debris piles, <10 m^2, were used by small mammals as frequently as the largest piles, >100 m^2. Small mammals were captured at debris piles as far as 107 m from the forest edge but distance from the forest was not a significant predictor of small mammal patterns.

Discussion

Piles of riverine woody debris, deposited in the riparian zone, are a common, natural feature of Pacific Northwest ecosystems. Debris piles can be enormous, with a footprint of over 500 m^2, and, once established, may withstand large flood events and become long-term features of the riverine landscape. As indicated by location and age of current vegetation, many debris piles in this study are older than 30 yrs. These debris piles have internal temperatures that are cooler than the ambient environment and provide a physical structure that enables resting and hawking by many species of birds. Small mammals were captured at debris piles in both the spring and fall, confirming that these piles are used by small mammals over the breeding season. Capture rates were higher at debris piles than at similar reference sites on the cobble bars suggesting that they might be important habitat components worthy of further investigation.

Despite their barren appearance, cobble bars are plentiful sources of insects (Rector 1991) and birds or small mammals may use debris piles to take advantage of these food resources. The physical structure of woody debris might even increase the availability of food resources, such as fungi, insects, and seeds, on the cobble bars. Debris is often ripe with fungal spores when initially deposited (Shearer and Von Bodman 1983) and these fungal colonies may grow and flourish over time. The availability of insects can be enhanced by the presence of debris piles. For example, insect populations recover from disturbances more quickly in the presence of woody debris (Anderson 1992). And, the piles create wind eddies that may aid in depositing airborne fungal sporocarps, and light seeds (Mason and Koon 1985).

The Use of Debris Piles by Avifauna

The physical structure of debris piles was used by a variety of avian species. Over 16 species of birds were observed landing on the debris piles (Table 1A). Many other species of birds were observed or heard in the study area but were never seen using the debris piles (Table 1B). Overall, 57% of the species detected within the study area were observed on the debris piles.

Whether or not an individual from a particular species was observed on a debris pile could often be explained by functional feeding guild (Table 1). Of the species heard in the area but not seen on a debris pile, 33% belonged to feeding guilds never observed using debris piles (insectivorous shoreline gleaner, carnivorous ground scavenger, carnivorous ground hawker, piscivorous water foot-plunger). Another 33% were insectivorous canopy-gleaners. Only one insectivorous canopy-gleaner, a black-throated-gray warbler, was observed on a debris pile.

Birds used the debris piles for a variety of common activities. The majority of bird use required only the physical structure of the debris. These activities included perching, hawking, and hopping. Other observed activities were territorial; birds sang, called, and chased each other from perch to perch. Foraging was observed in some cases but the food itself could not be identified. A few birds were also observed entering inside the debris piles. The use of the internal space is interesting because, previous to this study, bird use of similar internal environments has not been well-documented.

The Use of Debris Piles by Small Mammals

Over all three surveys, capture rates at debris piles were higher than those reported by McComb et al. (1993) for riparian forests in the Oregon coastal forests. Data from the spring and fall surveys display an increase in both species richness and abundance over the summer months. This change

reflects population increases over the breeding season that result in an increased use of all habitat.

In the final trapping, the interesting comparisons are between debris piles and reference sites on the cobble bars. Few mammals (either number of individuals or number of species) were captured at reference sites on the cobble bars, suggesting that debris piles may be important in allowing small mammals to venture onto or to inhabit the cobble bar.

It has been suggested that small mammals captured on cobble bars reside in the forest but are captured during foraging expeditions (Rector 1991). If this were true, we would expect the number of small mammals found on cobble bars to decrease with increasing distance from the forest edge. However, our results did not show a relationship between small mammal abundance at debris piles and distance from the forest for all small mammals together or for *P. maniculatus, P. keeni*, *Microtus*, or *Sorex* when analyzed individually. These findings suggest two possibilities; small mammals reside in the forest but debris piles provide enough shelter for them to forage far from the forest edge (> 107 m) or that small mammals reside in the debris piles on cobble bars.

Our results indicate that debris piles, an often over-looked component of riparian corridors, are used by both birds and small mammals. Debris piles may provide particularly valuable resources on cobble bars where they add to the structural complexity of the habitat. On cobble bars, they are used for perching and hawking by birds. Small mammals were found in greater numbers at debris piles on cobble bars than at reference areas. Further research to investigate woody debris piles may yield insights into which attributes are most attractive to particular species of wildlife. It is possible that some species may be dependent on this component of the riparian system.

Acknowledgements

The authors are grateful to Douglas G. Sprugel, Douglas A. Maguire, Jon A. Wellner, Alice Shelly, Tamre Cardosa, David A. Manuwal, and Jim Doyle for their assistance and advice with both the project and the analyses. We offer special thanks to Paul Schiffhauer, Dave Rolph, Aaron Inman and Sherry Hudson for their assistance with fieldwork. Research support was provided by the U.S. Forest Service, Pacific Northwest Research Station, the Center for Streamside Studies, and Ecosystems Northwest, University of Washington.

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Received 7 July 1998
Accepted for Publication 25 February 1999

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Effects of Stand Age, Size, and Juxtaposition on Abundance of Western Redback Salamanders (*Plethodon vehiculum*) in Coastal British Columbia

Abstract

Terrestrial-breeding amphibians live at high densities, show strong site fidelity, and have relatively stable populations, long life spans, and high vulnerability to dehydration. These traits make them potentially useful indicators of effects of canopy removal during logging. We compared the relative abundance of western redback salamanders (*Plethodon vehiculum*) in old-growth and managed second-growth stands on Vancouver Island, and found significantly more individuals in old-growth stands. Salamanders were more abundant in larger stands of old growth, but showed no relationship with stand or patch size among mature second-growth stands. Managed stands contained more salamanders when old growth was adjacent. Juvenile:adult ratios within managed stands were significantly higher in stands not adjacent to old growth, suggesting poor survivorship to adulthood in younger stands.

Introduction

Several studies have documented greater abundance of terrestrial salamanders in old-growth stands than in younger stands (Raphael 1988; Aubry and Hall 1991; Corn and Bury 1991; Dupuis et al. 1995). These observations have been interpreted as evidence that at least some recent amphibian declines are a result of habitat loss to forest practices (Welsh 1990; Johnson 1992). The rationale is simple. Terrestrial salamanders are susceptible to dehydration (Ray 1958; Spotila 1972; Feder 1983). Forest removal increases the risk of dehydration by increasing wind speed and radiation (Geiger 1965), and by reducing amounts of downed wood used as foraging and breeding sites (Bury et al. 1991; Welsh and Lind 1992; Dupuis 1997). Habitats that become unfavorable, even for short periods of time, are recolonized only slowly because of the low vagility or high philopatry exhibited by amphibians (Ovaska 1988; Welsh 1990). Thus, we expect to find greater amphibian abundance in relatively closed stands containing abundant downed wood; that is, in older stands.

Although there are differences between old-growth and young forests in the Pacific Northwest, few studies reveal strong trends in salamander numbers with stand age (Bury and Corn 1988; Bury et al. 1991; Gilbert and Allwine 1991). Bunnell et al. (1997) noted three possible reasons for differing results among studies: 1) variable amounts of critical elements such as downed wood or understory; 2) differences in regional macroclimates that determine importance of sheltering structures, such as overstory, understory, or downed wood; and 3) differences in the forest mosaic surrounding the study sites. Edenhamn et al. (1992), for example, suggested that patch size and isolation were critical factors governing effects of habitat fragmentation on amphibians. Here we examine potential effects of the forest mosaic; specifically, effects of stand age and size, and proximity of favored habitat. We report the relative abundance of amphibians in different sized stands of older forest, and in younger, managed stands with or without adjacent old growth.

Study Area

The study area was in the Coastal Western Hemlock Biogeoclimatic Zone near Port Alberni (49° 03'N and 125° 3'W), central Vancouver Island, Canada. This region receives more than 250 cm of precipitation annually (mainly in spring and fall), has a mean summer temperature less than 16° C, and a mean of 180 frost-free days per year (Meidinger and Pojar 1991). Stands were located in a 500 km^2 area and varied in elevation from 150 to 550 m above sea level.

We chose low to mid-slope, moist, nutrient rich, south-facing or flat sites that supported mixed

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TABLE 1. Characteristics of the sampling scheme.

Site[1]	Age (years)	Years Sampled	Number Plots[2]	Patch Size (ha)	Adjacent Old Growth[3]	
OG1	380+	'91 & '92	3	2500	extensive, contiguous	(Y)
OG2	330+	'91 & '92	3	800	extensive, contiguous	(Y)
OG3	500+	'91 & '92	3	90	> 10 km distant	(N)
M1	54	'91 & '92	3	1000	extensive, contiguous	(Y)
M2	60	'91 & '92	3	131	extensive, contiguous	(Y)
M3	72	'91 & '92	3	2000	ca 50 ha, > 300 m distant	(N)
Y1	17	'92	3	150	ca 750 ha, contiguous	(Y)
Y2	18	'92	3	50	extensive, contiguous	(Y)
Y3	18	'92	3	107	> 2 km distant	(N)
CC1	5	'92	2	58	extensive, contiguous	(Y)
CC2	5	'92	2	510	> 2 km distant	(N)

[1] OG = Old Growth; M = Mature, managed; Y = Young, managed; CC = Clearcut

[2] Each plot includes 45, 1x2 m quadrats (90 m^2)

[3] Y = Yes, old growth adjacent; N = no, old growth not adjacent for analyses of juxtaposition

stands of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). In 1991, we sampled old-growth (undisturbed) stands and 54 to 72-year-old (mature), managed second-growth stands to evaluate methodologies. In 1992 surveys were also conducted in 17- and 18-year-old (young) managed stands and in 5-year-old clearcuts. To avoid local microclimatic influences, all sites were located at least 30 m from temporary water bodies, 75 m from lakes and rivers, and 50 m from forest edges. Age and distance from water or forest edge were dominating criteria in site selection; the habitat mosaic permitted a range of stand sizes and some differences in isolation (Table 1). The mature stands were prescribed burned within 5 years of harvesting, and had regenerated naturally. The young stands were burned, planted, and subsequently mechanically treated to remove alder and smaller conifer stems.

Methods

From mid-May to mid-June 1991, we evaluated area-constrained searches over a range of plot sizes using Wiegert's two-term local quadrat variance methods (Krebs 1989:68; Ludwig and Reynolds 1988:43). Optimal plot size for assessing terrestrial salamander abundance proved to be 1 x 2 m (Dupuis et al. 1995); mean times for a thorough search of a 1 x 2 m plot were 9.3 minutes in old growth and 8.7 minutes in managed, mature second growth. In 1992, the optimal plot size was extended to young managed stands and clearcuts. Three study sites for each forest age class were selected, and studies were carried out in three, 2-ha plots (400 x 50 m) within each site or age-class replicate. Each plot consisted of 45, 1 x 2 m quadrats randomly placed, for a total sample area of 90 m^2 per plot. Total sample area within each study site was thus 270 m^2 (Table 1). We sampled one plot of 90 m^2 every 2 weeks from mid-April to late-May in 1992. We could sample only two recent clearcuts, each with 2 replicates.

Two people searched for salamanders, while a third handled the captures and recorded data. Searchers looked under all cover objects (logs, bark and rocks) and vegetation (ferns and moss), and probed all crevices. Captured salamanders were identified, sexed, weighed (±0.05 g) and measured (total and snout-vent length). Salamander age class was based on length distributions in Ovaska and Gregory (1989), who employed mark-recapture techniques with the same species (*Plethodon vehiculum*). We recognized three classes: hatchlings (<26 mm), yearlings or juveniles (26-35 mm), and mature (>35 mm).

To examine potential effects of stand age or habitat juxtaposition, analyses were site-specific and used the 3 plots per site as replicates. Where

2 years of data were available, two-way analyses of variance were initially performed to evaluate potential year effects as well as effects of forest age or patch size. Year effects were never significant, and subsequent analyses of relative density combined years. Potential differences among proportions of salamanders in different size/age classes were evaluated by Hicks' test of proportions. Fisher's exact test was used to test for potential influences of adjacent old growth on the relative numbers of juveniles and adults in younger stands.

Results

Average calculated densities (number/ha) of *Plethodon vehiculum* were 1519±145 (SE) and 1346±196 in old growth and 247±41 and 482±156 in mature second-growth during 1991 and 1992, respectively. Young stands and clearcuts were measured only in 1992, and yielded average densities of 247±90 and 28±28 (n = 4 plots), respectively. Because of high inter-plot variability (Figure 1a) there was no significant difference between sample years ($p > 0.15$). Density estimates for old growth were significantly higher ($p < 0.05$) than for the other three age classes. Only one salamander was found in the clearcuts; the 17-18 and 54-72 year-old age classes did not differ significantly.

Analysis of variance indicated a difference with patch size among old-growth stands ($p < 0.08$). Across both years mean relative densities in stands 800 and 2,500 ha in size, were 1611±174 and 1630±206 salamanders per ha, respectively (Figure 1b). The smaller stand (90 ha) had a relative density of 1056±178 salamanders per ha. Within mature, second-growth stands, there was no difference across stand sizes ranging from 131 to about 2,000 ha (Figure 1b). Nor were differences with size evident in young managed or clearcut stands.

There was little difference among proportions of hatchlings, juveniles, and adults with forest age class (Figure 2a). Across all years and forest ages, hatchlings represented 13% to 23% of the sample and juveniles usually comprised 11% to 26% (in 1992 they represented 40% of the mature second-growth sample). Tests of proportions revealed no significant differences in age class distribution with either forest age class or patch size ($p > 0.3$). There was, however, an apparent effect of stand adjacency. In 1991, mature managed stands with adjacent old growth had 13.2% young

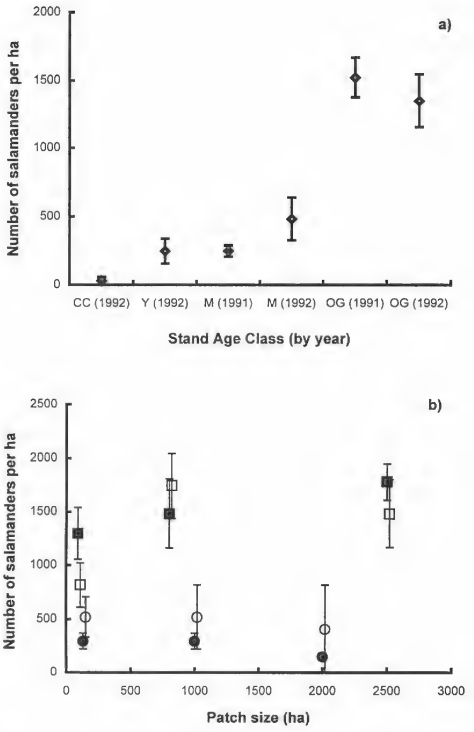

Figure 1. a) Relative densities of *Plethodon vehiculum* in stands of different ages. Values plotted are means and standard errors of 9 replicates (3 2-ha plots at each of 3 sites per age class). Recent clearcuts had only 4 replicates (Table 1). CC = clearcut (5 yrs), Y = young (17-18 yrs), M = mature (54-72 years), OG = old growth (300+ yrs).

b) Relative densities of *Plethodon vehiculum* in stands of different size and age. Means calculated as for a). Only 1 salamander was found in clearcuts. Old Growth 1991 (■), Old Growth 1992 (□), Mature 1991 (●), Mature 1992 (○).

(hatchling plus juvenile) salamanders, while mature managed stands without adjacent old growth had 75% young salamanders in the sample. The pattern was similar in 1992 (53% young with old growth adjacent; 88% young when not adjacent), though not as pronounced as in 1991 (Figure 2b). Two-tailed, Fisher's exact tests of the equality of proportions of young salamanders in mature, managed stands with and without adjacent old growth showed significant differences ($p < 0.04$). Of the young, second-growth stands (17 to 18 years

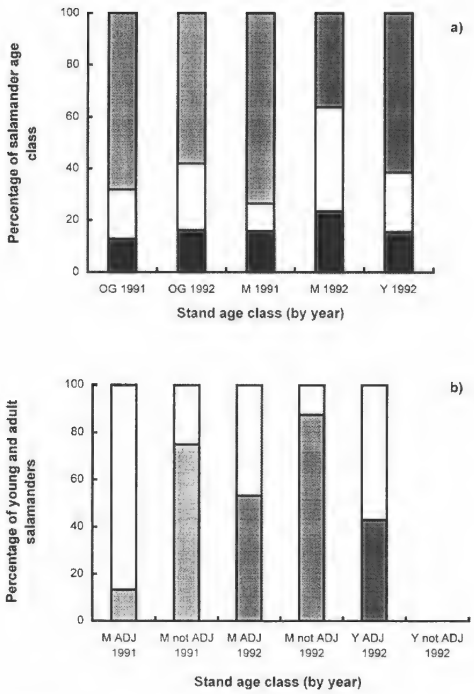

Figure 2. a) Percentages of adult, juvenile and hatchling salamanders in old growth (OG), mature (M; 54-72 years old), and young (Y; 17-18 years old) stands. Definitions of salamander age classes follow Ovaska and Gregory (1989). Grey bars represent the percentage of adults, white represent juveniles, and black represent hatchlings. b) Proportions of adult and young (juveniles and hatchlings combined) salamanders in mature (M; 54-72 years) and young (Y; 17-18 years) managed stands with and without adjacent old growth. No salamanders were encountered in young stands without adjacent old growth. White bars represent the percentage of adults, and dark bars represent young salamanders.

post-logging), only those adjacent to old growth contained salamanders, of which 43% were young salamanders. Only one salamander was encountered in clearcuts; an adult was found in the clearcut with adjacent old growth.

Discussion

We found a three- to six-fold difference in relative abundance of western redback salamanders between managed stands and old growth, with the lowest numbers in the youngest managed stands (Figure 1a). Although there are no consistent trends in relative densities of terrestrial amphibians with stand age (Bury et al. 1991; deMaynadier and Hunter 1995), in several studies individual species were more abundant in unmanaged or old-growth stands than in younger, managed stands (e.g., Means et al. 1996; Bunnell et al. 1997). In the Pacific Northwest these include: clouded salamanders (Corn and Bury 1991; Gomez and Anthony 1996); ensatinas (Raphael and Barrett 1984; Welsh and Lind 1988; Corn and Bury 1991); Del Norte salamanders (Raphael 1988; Welsh and Lind 1988,1995); Dunn's salamanders (Vesely 1996); northwestern salamanders (Aubry and Hall 1991); western redback salamanders (Corn and Bury 1991; Vesely 1996; Dupuis 1997); and Larch Mountain salamanders (Herrington and Larsen 1985). Most of the plethodontid salamanders of the Pacific Northwest are more abundant in habitats common in old-growth forests (Blaustein et al. 1995). These salamanders may be particularly sensitive to canopy removal because they are less resistant to desiccation than many amphibians and require terrestrial breeding sites (often downed wood).

The adult densities we observed in old growth were similar to those obtained by Ovaska and Gregory (1989), also in old growth on Vancouver Island. They employed mark and recapture in two plots (100 m^2 and 200 m^2). The total numbers they captured during their 2-year study were naturally much higher than we obtained during area-constrained searches (single search period). Extrapolating their more comparable, quadrat-based estimate of 28 salamanders on the 200-m^2 plot yields 1400 per ha; we estimated 1356 and 1519 per ha. In both years on our plots, numbers were markedly lower in managed stands, even those 54-72 years of age, than in old growth (Figure 1a). Current conditions do not appear to explain the large difference. There was little difference in amounts of downed wood across stand age (Dupuis 1997), and all sites were classified as "moist" or "very moist" in the same biogeoclimatic subzone (Meidinger and Pojar 1991). Moreover, by age 50 overstory effects on near-ground microclimate should differ little from old-growth stands. Combined, these observations suggest some prior, but long-lasting effect reduced salamander abundance in managed stands. Working in unmanaged stands of fire origin, Aubry and Hall (1991) found that western redback salamanders

were more abundant in young, than in mature or old growth stands. We cannot evaluate whether the different findings are a product of scale of initial opening (Aubry and Hall's stands were much smaller than ours), different structural legacies after fire than after logging, or some other influence.

Forest practices have altered the age structure of forests in the Pacific Northwest dramatically (e.g., Harris 1984; Wallin et al. 1994; McGarigal and McComb 1995). It was difficult for us to find low-elevation, old-growth stands on Vancouver Island in which to conduct this study and spatial distribution of stands could not be controlled. As a result, both old and young stands differed in their degree of isolation from nearby old growth (Table 1). We chose to group young stands as those with adjacent old growth and those without (the closest old growth was >300 m away). The smallest old-growth stand (90 ha) was also the most isolated (no other old growth within 10 km). Despite this natural variability and sparse data, some relations were statistically significant.

The effect of patch size among old-growth stands appears curvilinear (Figure 1b), as would be expected if some microclimatic or edge-related phenomenon were acting as an influence on populations. Changes in radiation and wind regimes induced by clearcutting extend about 50-100 m into adjacent forest (review of Bunnell et al. 1998). In even the smallest stand, there should be an unmodified area of about 50 ha in the stand core (where our study plots were located). It is thus unclear why there should be an apparent effect of stand size in our sample. Two influences are plausible: local microhabitat variation among stands, and broad-scale influences related to salamander movement. In terms of microhabitat the smallest old-growth patch contained the highest volume of downed wood, but was subject to flooding. Soil profiles contained considerable sand that would not favor plethodontid salamanders. This stand also was the most isolated from other old growth (Table 1). Bunnell et al. (1997) argued that movements of amphibians are often underestimated. Some species may depend on movement across larger areas than has been supposed, thus requiring larger areas of suitable habitat. If that is true, more isolated stands should appear as population sinks.

Older managed stands without adjacent old growth had significantly greater proportions of young salamanders than did stands with adjacent old growth (Figure 2b). A high proportion of young salamanders could be consistent with a thriving population, but not when densities are as low as they were in mature, managed stands (Figure 1a). Managed stands may be "sinks" with moderate reproductive success but poor survival to adulthood. Recolonization by adults from adjacent old growth may be important, but is likely to be slow given the low vagility of salamanders. This suggestion is supported by findings in young managed stands without adjacent old growth (no salamanders) and recent clearcuts (one salamander). The smallest and most isolated patch of old growth (90 ha) displayed both the lowest abundance and lowest amphibian richness of all old-growth patches (Dupuis 1993). We cannot separate fine-scaled microhabitat effects from broad-scaled habitat juxtaposition. Both are likely acting, but findings are more consistent with broad-scale effects.

Lehmkuhl et al. (1991) also attempted to evaluate broad-scale effects on western redback salamanders. They noted that their findings were somewhat contradictory in that salamander abundance was positively correlated with dominance of late-successional stages at the landscape level, but negatively correlated with the abundance of old growth in the "buffer" surrounding the stands they sampled. Broad-scale results are invariably difficult to interpret. Findings of Lehmkuhl et al. (1991) could reflect species packing in stands when surrounding old growth was less abundant (in which case they are similar to ours), or a preference by western redback salamanders for younger stands as documented by Aubry and Hall (1991) who worked in the same area (in which case they are contrary to ours).

Our data suggest that clearcutting greatly reduces the abundance of western redback salamanders, and that these effects are long lived. Adults are present in stands 17-18 and 54-72 years after clearcutting, which indicates that harvest practices did not locally eliminate the species. Adults represented a greater proportion of the population in stands adjacent to old growth, and recolonization did not occur readily unless there was old growth nearby. That suggests two options for retaining higher densities of terrestrial

salamanders: 1) extensive tracts of unmanaged forests (about 100 ha), or 2) retention of small patches of older forest within harvested areas. We could not separate potential impacts of reduction in downed wood and altered microclimate, so can offer no recommendations on patch size. In moist, coastal areas it seems likely that breeding sites are more important than microclimatic effects, so even small, undisturbed patches would be helpful provided they were not too distant from each other.

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Acknowledgements

The Canadian Natural Science and Engineering Research Council and BC Ministry of Forests supported our research. Sproat Lake Division of MacMillan Bloedel Ltd. provided logistic support. Comments by Bruce Bury and an anonymous reviewer improved the manuscript. This is Publication No. R-23 of the Centre for Applied Conservation Biology.

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Received 13 October 1998
Accepted for Publication 10 January 1999

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Effects of Collection Method on Sex and Age Composition of Black Bear (*Ursus americanus*) Harvest in Oregon

Abstract

We investigated sex and age distribution of 5168 black bears (*Ursus americanus*) harvested or live-trapped in Oregon from 1983 through 1994. Successful hunters were asked to submit a lower premolar tooth along with information on date, management unit, sex of the bear and method of take (i.e., using hounds, bait stations or stalking). In addition, we used capture records and tooth samples of bears snared following complaints of damage or live-trapped in two research studies. Tooth collections of hunter-harvested bears represented 5% to 58% of the annual harvest, as estimated from standard hunter phone surveys. Using data from all years, we compared frequency of sex and age classes according to method of harvest (i.e., hounds, bait, stalking, damage removal or live-trapping). More that 60% of bears harvested were males. Hunting with hounds accounted for >50% of the total harvest. Hunting method affected the proportion of males taken. The median age of bears harvested using hounds was greater than for baiting and stalking. Bears from damage removals and the live-trapped sample were older than those taken by stalking and while using bait stations. Our samples indicate different vulnerabilities of the sexes to different collection methods. Vulnerability ratio coefficients for male bears (compared with females) ranged from 1.46 (bait) to 1.12 (damage removals). We conclude that bear harvest data have a considerable age and sex bias, depending on collection methods used. This is likely to confound estimation of effects of changing harvest strategies, such as the prohibition of certain hunting techniques.

Introduction

The black bear (*Ursus americanus*) is an important big game resource in Oregon. During 1983-1994, an average of 22,015 (SE=1,106) bear tags were purchased annually by hunters, providing more than $220,000 in annual revenue for wildlife management to the Oregon Department of Fish and Wildlife (ODFW). Oregon=s bear populations appear stable and there are growing concerns about bear damage to livestock, timber and agricultural crops since 1983 (D. G. Whittaker, ODFW bear program coordinator, pers. comm.). Bears are hunted for one to two months in the spring on a limited entry license, and for three months during the fall on a general license. Prior to December 1994 bears could legally be harvested using hounds, bait and traditional stalking methods. However, use of hounds and bait was outlawed in December 1994 by voter initiative (Oregon Measure 18, hereafter called measure 18). In addition, special permits are issued to landowners experiencing damage to forest stands, crops or livestock. Because of their secretive habits and forested habitats, black bears are difficult to survey. Population estimation using mark-recapture studies are costly and often do not provide the necessary information in time for management decisions. Consequently, age and sex composition of harvested bears is used by wildlife managers as an index to population status, but the biological interpretation of such information is often not trivial.

In this paper, we present a case study of biases in hunter-harvested samples of large mammal species and the applicability of harvest data as indices for population management. In particular, we were interested in determining if harvest data are sufficiently unbiased to allow inferences about the population=s response to management. Because Measure 18 effectively eliminated the primary methods for harvesting bears, we tested the assumption that different methods do not affect composition of harvest and thus might be a random sample of bear populations statewide. We analyzed age and sex composition of harvested black bears in Oregon since 1983, to (1) compare sex and age composition associated with different collection methods, and (2) to evaluate if these data allow measuring potential impacts to Measure 18 on bear populations.

Methods

From 1983 through 1994 and estimated 14,785 bears were legally harvested in Oregon. Our sample contained 3811 hunter harvested bears for which

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age, sex and harvest method was known. In addition, we used age and sex structure of 1,263 bears taken by Animal Damage Control (ADC) personnel following damage complaints and 94 live-captured bears from two field studies for comparison. Bears inflicting damage to timber stands were primarily snared, while bears involved in livestock depredation were primarily removed using hounds. All bears taken upon damage complaints or live-trapped for research purposes were examined by ODFW biologists or ADC personnel, who extracted teeth and determined sex of bears. Prior to 1987, a volunteer program existed where bear hunters that submitted a harvest report card received a tooth envelope. The hunters were then asked to return the envelope with a premolar tooth and state the sex of the harvested bear and whether they used hounds or not. Beginning in 1987 successful hunters were asked to submit harvest information and a premolar in a special envelope issued with their tag. Before 1987, data contained information only on whether hounds were used or not. After 1987, bears harvested by stalking and hunting over bait were identified. Based on telephone surveys of hunters, 39.3 ± 8.6% of all successful bear hunters submitted a tooth after 1987. Bear teeth were sectioned and aged using the cementum annuli method (Willey 1974) at a commercial laboratory (Matson's Laboratory, Milltown, MT). Samples were sorted by season and collection method (hunted with hounds, hunted over bait, hunted while stalking, hunted without hounds, taken following damage complaints or live-captured for research purposes). We eliminated teeth from analysis if the collection method was not specified.

Because the resolution of collection information changed during our study, we tested for a significant effect of sampling period (i.e., 1983-1986 and 1987-1994, respectively) on age distribution of bears. Sampling period and interactions with collection method and sex did not contribute to model variance ($P > 0.05$), thus all harvest records were pooled. We used a Z-test of binomial proportions (Snedecor and Cochran 1980) to determine if sex ratios (proportion of males in the harvest) differed among collection methods. We used a linear regression of log-transformed frequency data for bears 3-22 years old to estimate instantaneous harvest mortality rates for each method of take (Bunnell and Tait 1980). We calculated the ratio of slope estimates for male and female (β_m/B_f) bears as an index to relative vulnerability of the sexes to different collection methods.

We used analysis of variance to detect effects of hunting/trapping method on age of bears. Because age frequency distributions of harvested bears were left-skewed, we used their median values as a measure of central tendency. We obtained the distribution of median ages for each sex and collection method by drawing 1,000 replications of a bootstrap sample comprising 100 records randomly selected from the original data set (with replacement). The distribution of median ages for each cohort was tested for normality and used a simple one-tailed t-test to test for differences among median ages. We accepted a type-I error rate of 0.05 for all tests.

Results

Bears taken from 1983 through 1994 in Oregon were predominantly male. Sex ratio of bears in damage removals was higher (71.3 ± 0.1% males) than the sex ratio of hunter harvested bears (64.3 ± 0.7% males, $Z = 2.68$, $P < 0.005$). Male bears also dominated the sample of bears live-trapped for research purposes (60.64 ± 0.06%), but there was no difference in the proportion of males compared with the hunted sample ($Z = 0.55$, $P > 0.05$), or damage removals ($Z = 1.71$, $P > 0.05$). Collection method affected the proportion of males taken by bear hunters, those using bait harvested a higher proportion of males than hound hunters (71.90 ± 0.22% vs. 64.09 ± 0.11%, $Z = 2.54$, $P < 0.005$). Bait hunting also resulted in a higher proportion of males than hunting by stalking (71.90 ± 0.22% vs. 61.4 ± 0.22%, $Z = 2.54$, $P < 0.005$). We suspected that spring bear hunters employing stalking would be more selective than stalking hunters in the fall, when bears may be taken incidentally while hunting other big game. However, there was no difference between the proportion of males harvested by stalking in spring (79.5 ± 6.8%) and fall (71.9 ± 2.7%, $Z = 0.96$, $P > 0.05$). Sex ratio of bears harvested with hounds did not differ from those harvested by stalking ($Z = 0.84$, $P < 0.05$).

Method of take and sex of harvested bears were significant factors determining the age of harvested bears ($F_{method} = 7.98$, $P < 0.0001$, $F_{sex} = 18.44$, $P < 0.0001$). Median age was greater for females than for male bears taken after damaging property (4.25

TABLE 1. Means of 1000 bootstrapped median ages of bears taken by different methods, and relative vulnerability coefficients for male black bears to different collection methods in Oregon, 1983-1994. Vulnerability coefficients are calculated for each collection method as the ratio of slope estimates ($\beta_{males}/\beta_{females}$), resulting from linear regression of log-transformed counts (frequencies) over ages of harvested bears.

	Hounds	Bait	Stalking	Damage	Live Capture
			Median Ages:		
Males	4.004 ± 0.004	3.034 ± 0.033	3.006 ± 0.018	3.901 ± 0.010	4.612 ± 0.027
Females	5.192 ± 0.155	3.611 ± 0.254	4.402 ± 0.281	4.250 ± 0.014	5.407 ± 0.021
			Vulnerability Coefficients:		
$\bar{x}$ ± S.D.	1.47 ± 0.31	1.44 ± 0.25	1.12 ± 0.10	1.22 ± 0.13	1.25 ± 0.72

± 0.01 vs. 3.90 ± 0.01 years, t = 20.97, P < 0.0001) and live-trapped bears (5.41 ± 0.02 vs. 4.61 ± 0.03 years, t = 23.51, P < 0.0001). Differences in median ages between male and female bears removed after damage complaints were lower than for any other method (Table 1). Similarly, median age of bears differed according to sex and hunting method. In general, hound hunters took older bears (male and female) than hunters using bait or stalking (Table 1). When using hounds, hunters killed younger males than females (t = 94.13, P < 0.005), and males harvested over bait were younger than females (t = 34.07, P < 0.005). Hunters stalking bears harvested younger males than females (t = 80.78, P < 0.005), but this tendency was not uniform among spring and fall seasons. In spring, male bears harvested by stalking were older than females (t = 17.01, P < 0.05) but the sample was small (n = 44). Live-trapped bears and those taken by using hounds were the oldest bears in our sample, while those harvested by bait and stalking were younger.

Vulnerability coefficients, based on ratio of instantaneous harvest rates of male and females showed pronounced variation with collection method (Table 1). Vulnerability to harvest was always higher for males than for females. Males appeared most vulnerable to hunters using bait and stalking methods. Hound hunters took relatively larger proportions of females, thus male vulnerability to hound hunters was lowest. Trapping methods such as damage removals and live-capture for research purposes exhibited intermediate vulnerability coefficients.

Discussion

Collection methods employed in Oregon had a significant effect on the sex and age composition of harvested black bear. Harvested black bears contained more male bears than females, and harvested males were younger than females. A heavy male bias in harvested black bears has been reported by other workers (Lindzey and Meslow 1980, Kane and Livaitis 1992, Litvaitis and Kane 1994). This may be due to legal protection afforded to sows with cubs, which may constitute a substantial portion of the female segment of a population. Male black bears in Oregon were significantly more vulnerable to harvest or trapping, and their vulnerability differed among collection methods. Not surprising, sex-specific vulnerability was lowest for hound hunting, where hunters were probably most selective for large bears (Bunnell and Tait 1980, Litvaitis and Kane 1994). However, we found no difference between proportions of males taken by hound hunters (most selective for large bears) and by ADC removals (least selective), and male vulnerability to both methods appeared similar. Similar to our findings, hunters who used stalking methods in New Hampshire (Litvaitis and Kane 1994) harvested lower proportions of male bears and some of the youngest bears, indicating that stalking hunters probably were less selective than hunters who used hounds and hunters using bait. We found that hunters that used stalking methods took older males than females during spring seasons (when bears were the sole species hunted), but the opposite trend was evident during the fall season, where hunters may take bears incidentally while pursuing other game mammals. This difference may be due to differential emergence and movement patterns of the sexes following hibernation. Bait and stalking techniques resulted in the highest proportion of males in the harvest and consequently the highest vulnerability ratio for males. Male home ranges tend to be larger than those of females

(Fraser et al. 1982), hence males should be more likely to encounter bait stations, baited trap sites or stalking hunters. We conclude that the available harvest data does not allow for separation of the effects arising from the legal protection of sows with cubs from those arising from hunter selectivity and bear vulnerability to harvest methods.

If harvest data are to be used as a representative sample of population structure, the sampling process must be random to produce unbiased sex and age structure information. This problem has long been recognized in fisheries management, where selectivity of fishing gear is considered a significant source of bias in stock assessments (Beamesderfer and Rieman 1998). Similarly, the development of capture models with unequal catchability corrections has occupied biologists and statisticians for decades (Pollock et al. 1990). If hunters are selective, or different age classes of animals differ in their vulnerability to harvest, the sampling process is no longer random, and estimates of population statistics are biased. For ungulates, harvest age structure and harvest sex ratio analysis of white-tailed deer (*Odocoileus virginianus*) have been shown to be severely biased due to differential vulnerability of various sex and age classes, and hunter selectivity (Roseberry and Woolf 1991). The pronounced differences in age and sex composition among different sampling methods of bears in Oregon indicated that substantial biases were inherent in hunter-harvested samples, which could affect management decisions. Without harvest-independent samples the true composition of the population cannot be estimated. Alternative methods, such as mark-recapture, are necessary to estimate age and sex-specific survival rates of black bears. Unless sources of bias (hunter preferences, bear behavior toward traps or bait) are known, estimates of population structure derived from harvest statistics appear unreliable. Detection of population responses to change in harvest regimes or hunting methods may be difficult.

We conclude that harvest data of black bear (and many other mammal species) are of questionable value for the assessment of population demography, unless they are confirmed by independent estimates of population composition and growth. We suggest that instead of relying on a single harvest statistic, wildlife managers should attempt to minimize data biases by obtaining precise estimates of total harvest, the harvest effort expended, and the sex-age structure of the harvest. Ancillary data, such as spring body condition indices, reproductive output of females and survival can facilitate the application of population modeling. We urge wildlife managers to consider functional, mechanistic processes of population regulation when making management decisions or assessing population status. Fundamental harvest theory, coupled with computer simulations and sound thinking can provide clues about the population's relative position along a yield curve. Lastly, we strongly recommend that wildlife managers employ adaptive resource management (Walters and Hillborn 1978, Lancia et al. 1996), using controlled harvest of wildlife as a deliberate experimental management action to test hypotheses regarding harvest effects and population regulation. Explicitly testing the effects of management actions can be an effective way of incorporating uncertainty into managing natural resources.

Acknowledgements

This study was supported by Federal Aid to Wildlife Restoration, Project W-87-R. Collaboration by ODFW biologists, ADC personnel, and the many hunters who remitted samples was greatly appreciated. We thank D. G. Whittaker, T. O=Neil, M. C. Boulay and D. K. Edwards for critical reviews of earlier drafts of this manuscript.

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Received 12 May 1998
Accepted for Publication 10 November 1998

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Correction

The following article, "Long-term Fire Incidence in Coastal Forests of British Columbia" by Kendrick J. Brown and Richard J. Hebda (pp. 41-43) is a corrected reprint of the same article printed in Volume 72, Special Issue No. 2, 1998, pp. 64-66. The article appearing in that issue had an incorrect graphic inserted for Figure 1. The article is reprinted in this issue with the proper figure.

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Long-term Fire Incidence in Coastal Forests of British Columbia

Introduction

Fossil charcoal and pollen records from five sediment cores were used to reconstruct the post-glacial fire and vegetation history on southern Vancouver Island (Figure 1). Specifically, macroscopic charcoal fragments representative of local fire activity were used to reconstruct the post-glacial fire intervals (Whitlock and Millspaugh 1996). Studies such as this are important because they provide insight to the projected changes in distribution, composition, and fire activity of future forests under a global warming climatic scenario (Hebda 1997, 1998).

Discussion

Following deglaciation, the landscape was characterized by a lodgepole pine (*Pinus contorta*) biogeochron between ca. 14 000 - 11 500 years before present (ybp) which experienced no fire, possibly because no ignition source existed or there was a lack of available fuel for combustion (Figure 2). Mixed forests consisting of lodgepole pine, spruce (*Picea*), fir (*Abies*), western hemlock (*Tsuga heterophylla*), mountain hemlock (*Tsuga mertensiana*), and alder (*Alnus*) replaced the lodgepole pine forests in the late Pleistocene and persisted until the start of the Holocene (10 000 ybp).

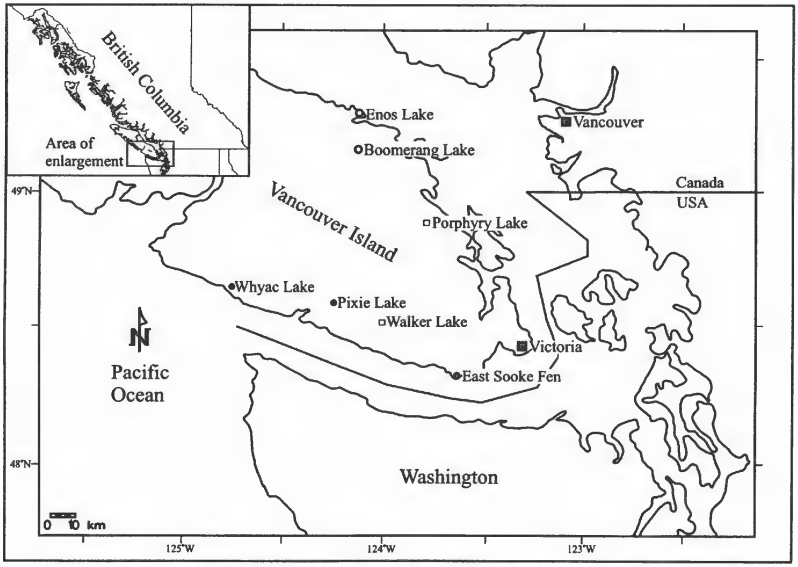

Figure 1. Regional location map showing sediment core sites analysed for both pollen and charcoal (●), charcoal only (○), and high elevation sites currently being analysed (□).

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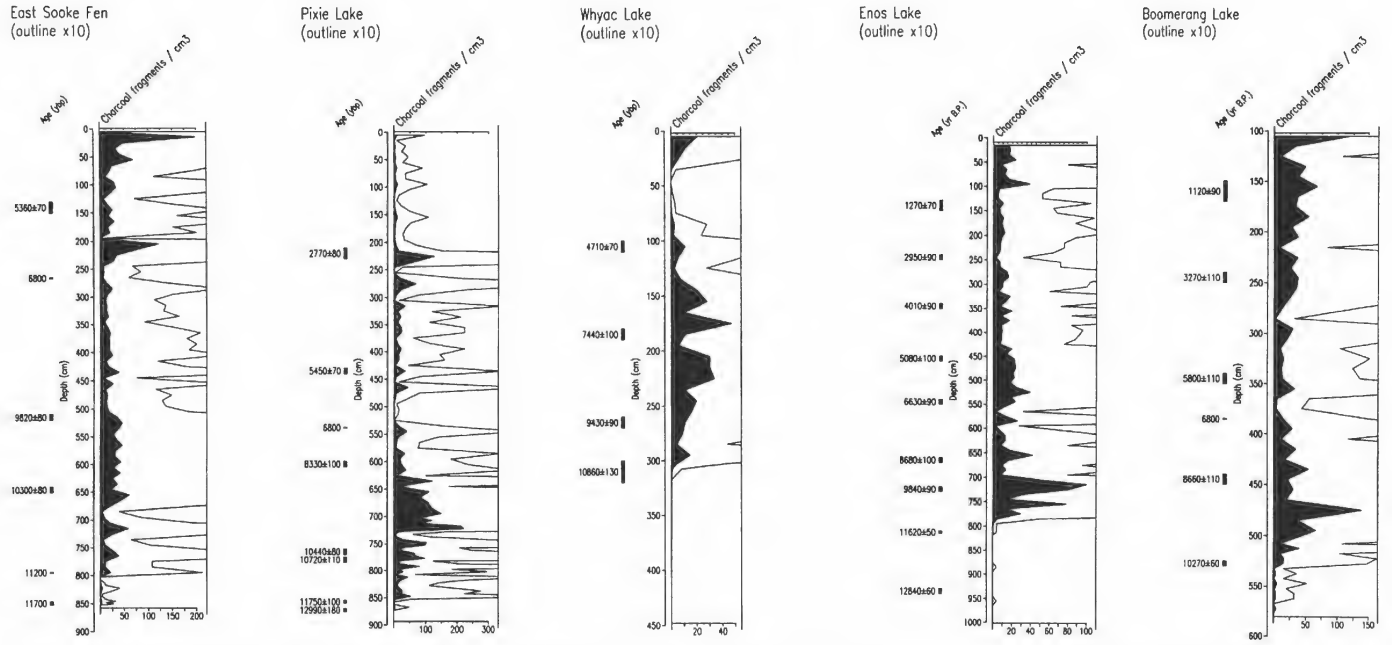

Figure 2. Charcoal profiles of sediment cores from Southern Vancouver Island. Ages are given in radiocarbon years. Sample beta numbers and descriptions are available upon request.

An increase in macroscopic charcoal concentrations at East Sooke Fen and Pixie Lake indicate fire became common during this interval. The early Holocene Xerothermic interval extended from 10 000 to 7000 ybp and is interpreted to have been 1-2°C warmer and drier than present (Hebda 1995). East Sooke Fen and Pixie Lake pollen records indicate Coastal Douglas-fir (CDF) biogeoclimatic zone-like (Meidinger and Pojar 1991) forests consisting of Douglas-fir (*Pseudotsuga menziesii*) and bracken fern (*Pteridium*) were present during this interval; whereas Whyac Lake, in a more moist climate, records Coastal Western Hemlock (CWH) zone-like (Meidinger and Pojar 1991) forests consisting of spruce, western hemlock, and possibly alder. A dramatic increase in the concentration of macroscopic charcoal fragments at Enos, Boomerang, and Pixie lakes during this interval suggests these areas experienced a profound increase in fire activity (Figure 2). Whyac Lake exhibits a minor increase in charcoal accumulation at this time. Surprisingly, charcoal concentrations remain low and even decrease in East Sooke Fen during the early Holocene, possibly because of taphonomic factors related to less rainfall for transporting charcoal, or because less forested landscapes produced fewer charcoal fragments. The warm dry early Holocene obviously experienced abundant fire and can be viewed as a 'pyrothermic' interval. Moister climate ushered in a warm wet Mesothermic interval at 7000 - 4000 ybp which was followed by neoglacial cooling between 4000 ybp and present. These moistening and cooling trends resulted in the establishment of CWH forests consisting of western hemlock and Cupressaceae species over most of southern Vancouver Island. An overall decrease in charcoal concentration suggests a regional reduction in either fire frequency or magnitude during this interval, although locally isolated fire events are evident in most sites (Figure 2). Charcoal-free intervals representing time intervals of ca. 3000 years occur at the more moist sites of Pixie and Whyac Lakes and imply that fire played a limited role in forest disturbance. However, the continuous deposition of charcoal at East Sooke Fen and Enos and Boomerang lakes suggests fires remained an important disturbance factor on the drier east side of southern Vancouver Island during the mid-to-late Holocene; the persistence of fire may be related to aboriginal landscape management practices at this time. A recent increase in charcoal concentration coincides with European settlement and landscape clearing.

Conclusion

Fossil charcoal and pollen collected from several sites around southern Vancouver Island show that vegetation composition and fire activity have varied considerably during the late Pleistocene and Holocene. Our results reveal that natural disturbance regimes of coastal forests were strongly shaped by climate, vegetation composition, and possibly human activity. Future forest disturbance and successional patterns may differ considerably from those of the recent past and become more comparable to those of the early Holocene Xerothermic or pyrothermic as the global warming trend progresses.

Acknowledgements

The authors kindly thank Forest Renewal BC and NSERC for providing funding. The University of Victoria also provided a Graduate Student Research Fellowship.

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Habitat Characteristics of an Intertidal Aggregation of Pacific Sandlance (*Ammodytes hexapterus*) at a North Puget Sound Beach in Washington

Abstract

Although the Pacific sandlance (*Ammodytes hexapterus*) is known to burrow into soft marine sediment to escape predation and conserve energy, few studies have examined its use of intertidal habitat in winter. I characterized intertidal sandlance habitat at a North Puget Sound beach in relation to tide height, oxygen concentration, and sediment size. The density of sandlance increased significantly as elevation in the intertidal decreased from 0.00/m^2 at 0.61 m above mean lower low water (MLLW) to 5.00/m^2 at -0.30 m below MLLW. There were no significant differences among depths to which sandlance were buried at three elevations (0.30, 0.00, and -0.30 m) in the intertidal zone (mean = 5.0 cm, range = 4.0 - 6.0 cm). The oxygen content of interstitial water at 0.30 m above MLLW tended to be lower at 6.0 cm (26.56 mm Hg) than at 4.0 cm (31.84 mm Hg) in depth but did not change during a low tide cycle when sediments were exposed to air. Additionally, there was no significant interaction between time of exposure and depth on interstitial water oxygen content. The oxygen tension of interstitial water at 0.30 m above MLLW was approximately one fifth of the saturated value (oxygen content of water in equilibrium with air) shortly after being exposed by receding tide and remained near this level until the site was reinundated with the incoming tide. This oxygen level is near the suspected anaerobic metabolism threshold for sandlance. Disturbances that lower interstitial oxygen levels or change the size of beach sediments could adversely affect intertidal aggregations of sandlance.

Introduction

Pacific sandlance (*Ammodytes hexapterus*) is found in coastal areas with soft sediments along the eastern Pacific Ocean from southern California to the Bering Sea (Hart 1973). The sandlance is an important prey item for a wide variety of birds, fish, and terrestrial mammals (Clemens and Wilby 1961, Shepherd 1988). During summer, sandlance may burrow into soft marine sediment for short periods to avoid predation (Raey 1970, 1973). It also may burrow at any time when prey (zooplankton) are unavailable. Since the sandlance does not have a swim bladder, energy is required to maintain position in the water column. Thus burrowing may conserve energy (Winslade 1974, Pearson et al. 1984, Quinn 1987).

Sandlance may also burrow into sediment during winter for relatively long periods of time. Healy (1984) showed that captive sandlance spent nearly three winter months in sand before emerging in spring to spawn. Winslade (1974) suggested that *A. marinus* overwinter in sand and use fat reserves acquired the previous spring and summer for maintenance of metabolism. The mechanism(s) causing these fish to enter this overwintering stage is still unknown, but Winslade (1974) suggested that it may be related to level of fat content in the fish and to local environmental factors such as low zooplankton density, low water temperature, and short day length.

Sandlance burrow into intertidal sediments of Puget Sound during winter months, presumably as part of an overwintering stage, although there is little information on this phenomenon. Sandlance aggregations may be susceptible to a variety of risks unique to their use of intertidal habitat such as predation from terrestrial predators (Dick and Warner 1982). In addition, disturbances that lower interstitial oxygen levels or change the size of beach sediments could reduce the ability of intertidal zones to support sandlance. However, to my knowledge no studies have examined how winter aggregations of sandlance use intertidal habitat in the Pacific Northwest. The objective of this study was to examine how sandlance use intertidal habitat during winter in relation to tide height, interstitial oxygen concentration, and sediment size.

Methods and Materials

Intertidal Distribution and Abundance

A pilot study was conducted in winter of 1985 to determine the general spatial extent of the intertidal

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sandlance aggregation at Clayton Beach. Clayton Beach is located in the southern portion of Larabee State Park on the northwest border of Skagit County, Washington (48°39'20" N Latitude and 122°29'30" W Longitude). I mapped 0.30 m elevation contours on Clayton Beach using a known elevation in the upper intertidal zone and a transit. All tidal elevations were based on mean lower low water (MLLW), which is the 19-year mean height of the lower of two daily low tides and defined as 0 m in elevation. Hereafter, all heights are in relation to MLLW. I began by digging holes (approx. 30 x 30 x 30 cm) at an elevation of 0 m in an area of intertidal zone where I had first located sandlance. I dug approximately 2 holes/m as I moved along the 0 m contour in both directions away from my starting point. I discontinued digging holes when I failed to find sandlance in the previous 15 holes. This transect gave me a crude estimate of the length (as measured along the shoreline) of the sandlance aggregation. To determine the width of the aggregation, I dug a series of holes (2 holes/m) along another transect perpendicular to the first transect. The second transect began at the approximate midpoint of the first transect and moved upslope. After locating the approximate upper elevational extent of sandlance on this transect, I dug a series of 5 continuous trenches (30 wide x 30 cm deep) from 0.30 - 0.65 m parallel to the second transect. These trenches were separated by approximately 10 m and evenly spaced along the length of the aggregation as determined by the first transect. My intent here was not to precisely measure the upper elevational limit of sandlance in this pilot study but rather to ensure that formal sampling (see below) would span the upper elevational range of sandlance. The pilot study showed that the upper elevation of sandlance was less than 0.61 m and concentrated in an area defined by approximately 50 m of shoreline (hereafter the study area). The study area was bordered by mud flats to the south and by a bedrock intertidal area to the north.

To determine how sandlance were distributed within the Clayton Beach study area, I used a stratified (by elevation) random sample design. In April of 1986, I established a 50 m transect along each of 4 elevation contours, 0.61, 0.30, 0.0, and -0.30 m. On each of the 4 transects, I randomly established 10 $1m^2$ plots in which I determined the density of sandlance. I constrained my study design such that half of the plots (5) per transect occurred on each side of a line perpendicular to the contours that divided the study area into roughly two equal parts. In this way I ensured that plots did not occur in an overly clumped fashion (J. Skalski, University of Washington, personal communication).

At each plot, I marked a square 1 m^2 area and removed all sediment to a depth of approximately 30 cm while capturing all sandlance. I removed sediment starting at the edge of the plot and working toward the center to minimize the amount of sediment sloughing from the edges, although this was not a major problem. During the excavation of sediment, I also determined the depth (n = 5 per transect) to which sandlance burrowed. I determined burrow depth by measuring the distance from the sediment surface to the deepest ventral surface of the fish. Sandlance are oriented horizontally in the substrate. I had relatively small sample sizes of burrow depth, in part, because it was difficult to uncover and measure the depth of buried fish without disturbing them. Exposing the head or otherwise disturbing (e.g. vibrations) buried fish would cause them to vigorously flop about leaving little or no trace of their previous position. While this behavior did not prevent me from catching disturbed fish, it made measuring burrow depth impossible. I was limited to measuring the depth of the few fish whose posterior end was haphazardly (fortuitously) uncovered while the anterior portion remained in the sediment.

In each instance where I measured the depth of a sandlance, I also noted the depth of the anaerobic zone. I used the first noticeable change in sediment color from light gray in the aerobic zone to black in the anaerobic zone, based on ocular estimate, as the point at which the anaerobic zone began (Fenchel and Riedl 1970, Jørgensen and Fenchel 1974). My intent here was not to determine the depth of anaerobic layer per se, but to note where buried sandlance were located relative to that layer.

Interstitial Oxygen Tension

I determined the oxygen content of interstitial water at each of two randomly located sites along the 0.30 m elevation contour in the study area. I withdrew interstitial water from depths of 4 and 6 cm at each site three times during a low tide cycle; immediately after the receding tide first exposed

the sites, when the tide was at its lowest point, and just before the sites were reinundated by incoming tide (approximately 2 hr intervals). I selected sites at 0.30 m because this was near the upper elevation of sandlance distribution, and depths of 4.0 and 6.0 cm because they represented the range of depths at which sandlance were found.

I sampled interstitial water using a 1 ml glass syringe connected to a modified needle with a short piece of latex tubing. The needle was made from a small diameter brass tube sealed at one end with solder and sharpened so that I could easily insert it into the sediment. Small bore holes, that allowed water but excluded sediment, were drilled into the tube near the sealed end. I inserted the needle to the appropriate depth and drew 0.95 ml of water into the syringe. The dead space in the needle and syringe (0.05 ml) had been previously filled with a saturated solution of NaCl, which has low gas solubility (Welsh and Smith 1960). After drawing a sample, I removed the needle, sealed the syringe with hematocrit sealer (wax), and stored the sample on ice for 2-6 hr. I determined the oxygen content of the water sample using a Corning Blood Gas Analyzer (model 175) and corrected the oxygen tension of the sample water for dead space volume in the syringe. To help determine if there was a decline in oxygen tension as a result of microbial respiration, I took two control samples of oxygen-saturated water from Clayton Beach using methods described above. One was held on ice for 2 hours while the other was held on ice for 6 hours. The oxygen tension of the 6 hr sample was 174.1 mm Hg versus the 2 hr sample of 177.8 mm Hg representing a decline of 2.1%. Based on this result, I assumed that the effect of microbial respiration on oxygen content of interstitial water was negligible.

I used nonparametric statistics when data were not normally distributed and when square-root transformed data (Zar 1984) did not improve normality as determined by Lilliefors test (Wilkinson 1992). I analyzed square-root transformed density (fish/m^2) data using analyses of variance (ANOVA) and Fisher's Least-Significant Difference test (Wilkinson 1992), which allowed for comparisons between treatment pairs when overall treatment affects were significant (i.e. $P < 0.05$). I analyzed fish depth data using a Kruskal-Wallis one-way ANOVA, and interstitial oxygen data using a 2-way (depth x time) ANOVA.

Intertidal Sediment Size

I returned to the Clayton Beach study area in May 1998 to characterize the type of substrate in which sandlance burrowed. I collected eight, 1 kg sediment samples from holes dug along the -0.1 m elevation contour in the general vicinity where I worked in 1986. Samples were collected only from the aerobic layer, which occurs just above a color change denoting a shift to anaerobic conditions, and only from holes in which I located one or more sandlance. I assumed that sandlance were using the same types of substrate in 1998 as they had in 1986. Sediment samples were dried, sifted through a series of sieves (5.6, 2.00, 1.00, 0.50, and 0.36 mm), and weighed to the nearest gram.

Results

Abundance, Distribution, and Interstitial Oxygen

The density of sandlance increased significantly ($F_{2, 27} = 16.09$, $P < 0.001$) as elevation in the intertidal decreased (0/m^2 at 0.61 m, 0.80/m^2 at 0.30 m, 2.40/m^2 at 0.0 m, and 5.00/m^2 at -0.30 m; Figure 1). There were no significant differences ($c^2_{0.05, 2} = 2.70$, $P = 0.26$) among mean depths of sandlance at three elevations (Figure 1). Sandlance were found at a mean depth (pooled for all elevations) of 5.0 cm ($SE = 0.2$ cm, range = 4.0 - 6.0 cm) and were always found above the anaerobic layer as determined by ocular estimate.

The oxygen content of interstitial water tended to be lower at 6.0 cm than at 4.0 cm in depth ($F_{1, 6} = 4.62$, $P = 0.08$) throughout the low tide cycle but did not differ as a function of time ($F_{2, 6} = 0.72$, $P = 0.52$). Additionally, there was no significant interaction between time and depth ($F_{2, 6} = 0.43$, $P = 0.67$; Table 1). The oxygen tension of interstitial water at 0.30 m was approximately one fifth of the level of oxygen-saturated water (oxygen content of water in equilibrium with air) shortly after being exposed by receding tide and remained near this level until the site was reinundated with incoming tide approximately 4 hr. later.

Intertidal Sediment Size

The sediment diameter in which sandlance were buried varied in size from approximately 10 mm to less than 0.36 mm. The majority of sediment, approximately 85% by weight, was between 0.36 - 1.00 mm in diameter (Table 2).

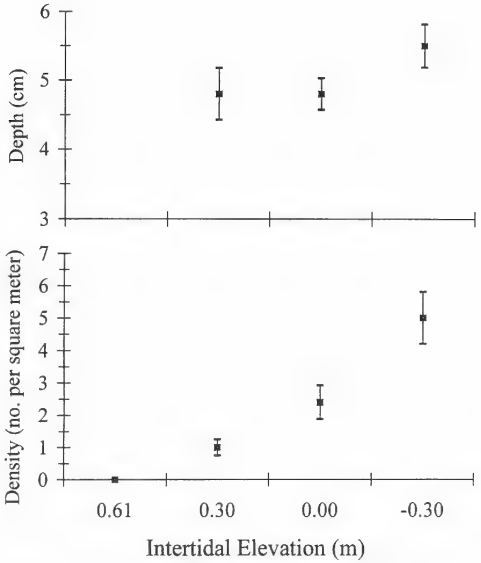

Figure 1. The density and standard error of sandlance (lower panel) and the depth and standard error to which sandlance burrow (upper panel) at Clayton Beach, Washington as a function of intertidal elevation.

TABLE 1. Mean oxygen content (and standard error), in mm Hg, of interstitial water from Clayton Beach at 0.30 m above MLLW as a function of time that elevation is uncovered by water during a low tide cycle.

Depth (cm)	N[1]	Cumulative time uncovered by water (min)		
		0	135	240
4.0	6	33.32 (5.95)	35.27 (1.01)	26.95 (3.90)
6.0	6	25.21 (0.47)	30.06 (1.53)	24.42 (0.42)

[1]Two water samples were taken per depth per time interval.

TABLE 2. Proportions (by weight in grams) of different sized sediments in the intertidal habitat of sandlance at Clayton Beach, Washington, 1998.

Sediment Size class(mm)	Proportion by weight (n = 8)	
	Mean	Standard error
>5.6	0.34	0.84
2.00 - 5.6	1.47	0.32
1.00 - 2.00	4.42	0.65
0.50 - 1.00	65.27	6.01
0.50 - 0.36	21.30	5.69
< 0.36	7.19	1.27

Discussion

The sandlance is an important component of the marine food web in Pacific Northwest waters (Pinto et al. 1984). In spring, sandlance use the upper intertidal zone to spawn and spawning beaches (where sandlance eggs are found) are fairly common in the Puget Sound (Penttila 1995). However, few studies have looked at how winter aggregations of sandlance use intertidal habitat. It is unclear, for example, if the sandlance overwinters in the same beaches it uses for spawning (D. Penttila, WA Dept. Fish and Wildl., personal communication) or whether intertidal sandlance aggregations are contiguous with larger groups of sandlance using subtidal habitat. I examined several aspects of intertidal habitat use by sandlance in winter, but since this study was limited to a single aggregation, conclusions based on this work should be made cautiously.

Sandlance respire interstitial water when buried (Quinn 1987) and like most other fish species maintain oxygen consumption independent of the ambient oxygen tension down to some critical oxygen tension (P_c). Below the P_c, when oxygen becomes limiting, sandlance probably turn to anaerobic metabolism, which in most cases is a short duration strategy, to make up for shortfalls in the aerobic energy production (Hochachka and Somero 1984). Sandlance are probably incapable of surviving long when oxygen levels go below their P_c, approximately 15- 31 mm Hg depending on temperature (Quinn and Schneider 1991). In cases where extreme low tides correspond with unseasonably warm weather, sandlance may emerge from the exposed sediment (Dick and Warner 1982), presumably because oxygen becomes limiting (Quinn and Schneider 1991), and either desiccate or become easy prey for a host of predators. Warmer temperatures have a dual effect on oxygen content of interstitial water; decreasing the solubility of oxygen in water and increasing the rate of microbial respiration that can deplete oxygen from interstitial water (Johnson 1965). Thus, the severest test of hypoxia tolerance for intertidal sandlance aggregations probably occurs during daytime low tides when sandlance cannot escape to better oxygenated conditions of the water column if interstitial oxygen becomes limiting.

The factors determining the local distribution of intertidal aggregations of sandlance are poorly

understood (Raey 1970). Dick and Warner (1982) found that intertidal aggregations of sandlance in Alaska were often associated with stream or river mouths, and further observed sandlance in brackish water indicating a tolerance for low salinity. Anecdotal observation from this and other studies suggest that intertidal aggregations near Bellingham, Washington are patchily distributed (D. Penttila, Washington Department of Fish and Wildlife., personal communication): a pattern that may be related to requirements for specific types of intertidal habitat. Oxygenation of the sediment is undoubtedly an important component of intertidal sandlance habitat. Sandlance in the North Sea and off Nova Scotia are found associated with the edges of shallow sand banks where strong tidal currents maintain well oxygenated surface sediments (Macer 1966, Meyer et al. 1979). Pinto et al. (1984) showed that sandlance avoided silt while preferring sandy to gravely substrate, a behavior they attributed to the greater availability of oxygen in sand. My study area was near the mouth of a small creek that goes subsurface when it reaches the beach. It is possible that this subsurface water helps make Clayton Beach suitable for intertidal habitat use by increasing the oxygen levels of interstitial water.

Sandlance were never found in the anaerobic sediment layer but rather occupied a narrow range of depths in the aerobic layer. Here, the sandlance experiences interstitial water with oxygen levels approaching its P_c. Although I could not show that the oxygen content of interstitial water was lower at 6 cm than at 4 cm in depth (i.e. $P = 0.08$), that conclusion is consistent with other studies of intertidal sediments (Gordon 1960, Brafield 1964). This narrow zone of habitat (4 - 6 cm) may represent a balance between the need for oxygen, which decreases with depth (although the effect of temperature may be inversely related to depth), and protection from surface predators which likely increases with depth. My results suggest that the oxygen content of interstitial water at Clayton Beach was at equilibrium since it did not change over the course of the low-tide cycle. If the pattern of oxygen availability is similar at all elevations (consistent with lack of relationship between buried depth and elevation), then one way to minimize the risk of hypoxia and thus predation is to burrow at lower elevations in the intertidal zone since time of exposure (i.e., uncovered by water) is inversely related to elevation. This may explain why sandlance density was inversely related to intertidal elevation but begs the question; what advantages, if any, are gained from burrowing into intertidal sediments at higher elevations?

If oxygen in interstitial water is limiting for sandlance, disturbances that affect availability of oxygen may have important consequences for intertidal sandlance aggregations. Upslope disturbances such as logging and urbanization can add fine sediments to streams (Bilby 1985). If deposited near the mouths of streams, these fine sediments could fill interstitial spaces and thus reduce the flow of interstitial water. The addition of organic materials (e.g. sewage) can increase the water's biological oxygen demand, which may lower interstitial oxygen levels (Waldichuk 1977). The sorting and distribution of beach sediments is a dynamic process of deposition and erosion (Downing 1983). It is possible that as shorelines are developed, the sediment characteristics of beaches that support intertidal aggregations of sandlance will change. Our near term task is to understand how human disturbance affects important components of the near shore ecosystem which includes intertidal aggregations of sandlance.

Acknowledgments

This study was done in partial fulfillment of the requirements for a M.S. at Western Washington University. I thank D. E. Schneider, J. Keyes, and L. M. Heggen for their assistance and St. Joseph's Hospital in Bellingham for use of their laboratory equipment.

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Received 30 June 1998
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Notes

Northwest Science Notes contains papers that are less than four pages long. There is no specific format or content required for articles, but all papers will be peer-reviewed and must be scientifically credible. Papers cover a wide range of topics and material of interest to our readers. The following inaugural article by Thomas N. Kaye is a good example of the kind of paper appropriate for Notes. Authors may contact the Editor about the suitability of manuscripts for this section.

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Obligate Insect Pollination of a Rare Plant, *Lupinus sulphureus* ssp. *kincaidii*

Fender's blue butterfly (*Icaricia icarioides* ssp. *fenderi* Macy) was presumed extinct until its rediscovery in 1989 near Corvallis, Oregon (Chambers 1990, Hammond 1991). This remarkable find has focused attention on the biology of its host plant, *Lupinus sulphureus* ssp. *kincaidii* [Smith] Phillips (Kincaid's lupine). Butterfly oviposition and larval development in the wild occur primarily on this rare plant. Occasionally, butterfly populations are also associated with *L. arbustus* Dougl. (spur lupine) and *L. albicaulis* Dougl. (sickle-keeled lupine), but only when *L. sulphureus* ssp. *kincaidii* is also present (Hammond and Wilson, 1993). Populations of *L. sulphureus* ssp. *kincaidii* are primarily restricted to grassland remnants in the Willamette Valley. Both the butterfly and the lupine are proposed for threatened or endangered species status by the U.S. Fish and Wildlife Service (Oregon Natural Heritage Program 1998). To develop conservation strategies for both organisms, research on the restoration of native prairie remnants and the biology of the lupine and the butterfly is underway (Schultz 1997, 1998; Wilson et al. 1997).

Excavations of caudices and root-systems suggest that *Lupinus sulphureus* ssp. *kincaidii*, a perennial, may spread vegetatively over limited distances (M.V. Wilson, pers. comm.), but sexual reproduction is necessary for population expansion and colonization of new sites. Any limit to seed production may restrict lupine population growth and, in turn, butterfly population success. If this lupine does not actively self-pollinate and self-fertilize, pollinating insects will be crucial for seed production. Also, seed production and dispersal may be limited by seed predators. The objective of this study was to determine if *L. sulphureus* ssp. *kincaidii* flowers set seed in the absence of insect pollinators and, secondarily, ascertain if seeds are killed by insects before seed dispersal.

Inspection of flowers (Kaye, personal observation) revealed a pump (or piston) arrangement for cross-pollination (as described by Knuth [1908]), in which a string of pollen is pushed through the tip of the keel by the stigma when the pistil comes under pressure during an insect visit. In this system, which is common in lupines, the stigma is protected from automatic self-pollination by a peristigmatic ring of hairs and possibly by protandry (Juncosa and Webster 1989). Most lupine flowers do not produce nectar, and

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insect visitors, normally bees, gather pollen (Knuth 1908). Flowers mature sequentially from the bottom to the top of each inflorescence, passing first through male then female phases. Lupine pollinators (such as bumblebees) often forage from bottom to top within an inflorescence (Haynes and Messler 1984). This system promotes outcrossing because insects laden with pollen from another plant contact female-phase flowers before traveling up to male-phase flowers where they collect pollen and depart.

The study population of approximately 75 plants was located in 1.5 ha of native prairie on a south-facing slope at Oregon State University's McDonald Forest, near Corvallis, Oregon. On 15 May 1990, single unexpanded racemes (all flowers in bud) were tagged on 30 individuals (plants typically produced 5-20 racemes). Fifteen racemes were selected at random and covered with a nylon mesh (0.5 mm) bag to exclude pollinators. The remaining 15 racemes were not covered and served as controls. The plants were checked biweekly during the course of the blooming season to observe pollinators (2-hr survey periods) and ensure that the racemes elongated normally in the bags. All marked racemes were gathered on 24 July 1990 when fruits were mature. The number of flowers and fruits per raceme were counted and fruits were inspected to determine ovule number and production of mature and damaged seed. Flower number was obtained from the number of pedicel scars on each raceme. Mean ovule and seed production per raceme were used for calculating mean and standard error (SE) for each treatment (n=15).

Lupinus sulphureus ssp. *kincaidii* did not set fruits or viable seed in the absence of pollinators. On average, open pollinated racemes displayed 75 flowers (range: 58-123, n=15), and bagged inflorescences had 73.2 flowers (range:44-99, n=15); there was no significant effect of bagging on flower production (t=-0.288, P=0.776). The average fruit on open pollinated racemes contained 4.5 ovules (range: 4-5). Fruit-set on open-pollinated (control) racemes was 4.3% (± 0.6% SE) and seed-set per fruit was 30.6% (± 2.5% SE). No fruits or seeds were produced on bagged inflorescences, apparently because mechanical or temporal barriers prevented self-pollination; genetic self-incompatibility is unknown in *Lupinus* (Arroyo 1981). Ovule predation (possibly by short-nosed weevil larvae) averaged only 6.1% (± 2.4% SE) per fruit in unbagged inflorescences. Overall, 46.7% of fruits were occupied by insect larvae. Therefore, predispersal ovule predation may not limit seed production or seedling recruitment at this site. At other sites, however, up to 85% of fruits can be damaged by insect larvae (K. Kuykendall, Oregon State University, pers. comm.).

The pump arrangement for pollination and the lack of fruit or seed formation in bagged racemes is strong evidence that insect pollinators are required for seed production in *Lupinus sulphureus* ssp. *kincaidii*. Studies of the annual *L. nanus,* a facultatively autogamous species, have also shown that excluding pollinators can reduce reproductive success (Karoly 1992). The present report of obligate insect pollination of *L. sulphureus* ssp. *kincaidii* does not explore whether or not this perennial is self-compatible. No gametic self-incompatibility system was found in *L. nanus* ssp. *latifolius* (Juncosa and Webster 1989), however, and selfing rates vary widely among species and populations of several annual lupines (Horovitz and Harding 1972; Harding, Mankinen, and Elliott 1974; Helenurm and Schaal 1996). Instead, floral anatomy and pollinator behavior and availability appear to play pivotal roles in promoting outcrossing in lupines (Juncosa and Webster 1989, Karoly 1992). This report documented the importance of insects as pollinators at only one site and in one year, and it is clear that the importance of insects can differ from site to site, at least in annual lupines (Karoly 1992). A genetic study (Liston et al. 1995) of *L. sulphureus* ssp. *kincaidii*, however, documented low inbreeding coefficients at several populations of this taxon, which is indicative of an outcrossed breeding system.

Conservation of *Icaricia icarioides* ssp. *fenderi* will require maintenance of viable lupine populations, which may require protection of populations of insect pollinators. The only insect observed visiting the lupine flowers at the study site was a single bumblebee (*Bombus* sp.). Average seed production was 1.3% of available ovules per raceme, despite a locally wet spring and apparently plentiful soil moisture, which is well below values reported for other lupine species (Wiens 1984). The reasons for this are not clear. Cool misty days, common in 1990 while flowers were at anthesis, may have impeded pollinator activity. Climate data from Corvallis, Oregon (Oregon Climate Service, www.ocs.orst.edu/) show that June of 1990 had above average precipitation and

below average maximum temperatures. Alternatively, native pollinators may be infrequent at the study site. If bumblebees or other insects that work the inflorescences from bottom to top are the typical pollinators for this species at most populations of *Lupinus sulphureus* ssp. *kincaidii*, then outcrossing is likely to be the dominant breeding system in this perennial lupine.

Acknowledgements

I wish to thank Mark V. Wilson of the Department of Botany and Plant Pathology at Oregon State University for encouraging me to submit this note for publication. Deborah Clark, Cheryl Ingersoll, Bob Meinke, and Mark V. Wilson made helpful comments on an earlier version of the manuscript. Reviews by Keith Karoly and Daniel F. Mayer substantially improved this paper. This is a publication of the Restoration and Plant Conservation Biology Cooperative Project, Oregon Department of Agriculture and Oregon State University.

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Received 30 April 1998
Accepted for publication 17 January 1999

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Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect) to the Editor.

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Requiem for a Sagebrush Ecosystem?

Early settlers crossing the Intermountain West described the Snake River Plain as covered by a vast sea of sagebrush, or wormwood (*Artemisia* spp.), as far as the eye could see (Frémont 1845, Yensen 1982). Today, anyone crossing that same area will find sagebrush in fragmented remnants and the vast sea is instead a grassland of an exotic annual, cheatgrass (*Bromus tectorum*). In little more than a century, the form and function of an entire landscape have been altered, perhaps irreversibly.

Fires, heavy grazing that severely disturbed soils and promoted cheatgrass invasion, and intentional eradication by "range improvement" programs had eliminated approximately 10% of the almost 60 million ha of big sagebrush (*Artemisia tridentata* spp.) communities by the mid-1970's (Vale 1974, Braun et al. 1976). If anything, the rate at which sagebrush is lost from these lands is increasing in recent years. In 1979, big sagebrush and native salt desert shrub communities in the Snake River Birds of Prey National Conservation Area, in southwestern Idaho, covered approximately 100,000 ha and comprised 51% of the total area. Because of fires and other disturbance, only 58,000 ha of shrubland remained in 1994 (U.S. Dep. Inter. 1996) (Figure 1). Another 12,000 ha of shrublands burned by 1998. Within the tenure of many land managers and biologists, the total grassland area had increased from 17 to 53% and more than half of the existing shrublands were lost. Shrubland losses in the National Conservation Area are typical of many sagebrush ecosystems in lower elevations and in xeric climates throughout the Columbia River Basin and Great Basin (Noss and Peters 1995). The changes are largely unnoticed among other more glamorous natural resource issues in the Pacific Northwest.

The Process of Losing an Ecosystem

Historically, fire was an important disturbance that maintained the dynamics between native grass and big sagebrush dominance in the ecosystem. Frequent small fires opened the shrub canopy and aided establishment of native perennial grasses at small scales, and created a mosaic of grass and shrub communities in different stages of development at large scales. Large catastrophic fires and reburning events, although present, were rare enough that shrub recolonization maintained the appearance of a vast shrubland landscape to early explorers and immigrants.

The dynamics of the system changed when cheatgrass invaded the sagebrush ecosystem in

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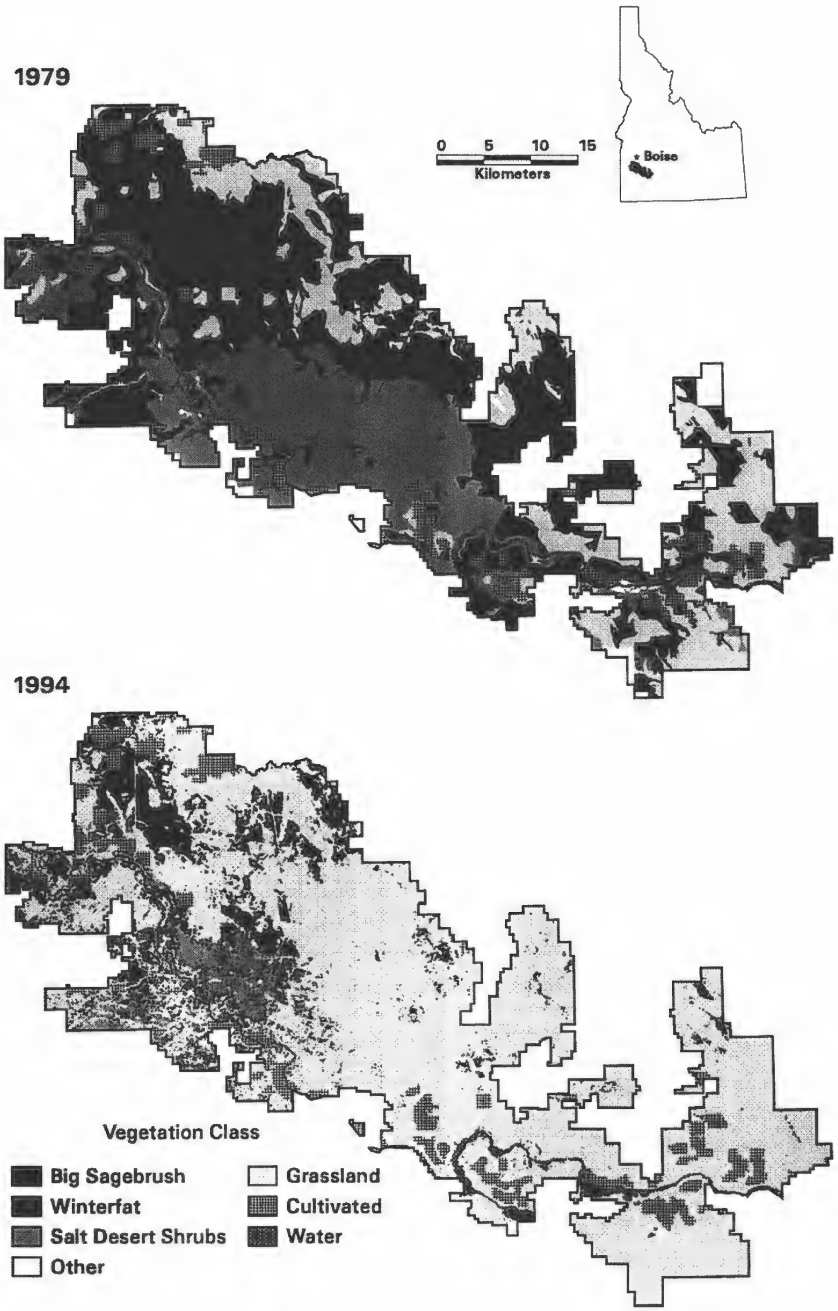

Figure 1. Habitat change and loss of shrublands in the Snake River Birds of Prey National Conservation Area, southwestern Idaho from 1979 to 1994. The 1979 map was delineated from aerial photography. The habitat map for 1994 was classified from Landsat thematic mapper satellite imagery.

the early 1900's. Cheatgrass expansion was aided by overgrazing, drought, agricultural practices, and natural and human-caused fires (Yensen 1981). The continuous fuels provided by cheatgrass, compared to more patchily distributed native bunchgrasses, facilitated fire spread and subsequent loss of shrubs (Klemmedson and Smith 1964). Large shrublands were fragmented and eliminated by an accelerating process of cheatgrass invasion and subsequent fire spread from grasslands into the shrub patch. Fires fragmented large shrubland areas into smaller patches, which increased the amount of grass and shrubland boundaries as well as the spaces between patches, and the patch ultimately was destroyed (Whisenant 1990, Knick and Rotenberry 1997). Thus, the role of fire has changed from maintenance to destruction.

Current Management

Managers currently emphasize fire prevention, suppression, and rehabilitation because fire is the most dramatic and visible factor changing these ecosystems. However, land uses that disrupt soils, increase erosion, and help establish cheatgrass synergistically increase the consequences of fire. In the National Conservation Area, regions that had combined fires, livestock grazing, or military training also had the most severe changes from shrubland to annual grasslands (U.S. Dep. Inter. 1996). We need to better understand how other disturbances interact to set up the system for greater consequences to fire.

The philosophy of "fuels management" and a strategy for prescribed fires is rapidly invading rangeland management from forestry dogma. These management actions must then be followed by efforts to control weeds, usually by herbicides, and reseeding. Without subsequent weed control, the process is doomed because we are using an intensive disturbance to eliminate or reduce vegetation that thrives on conditions following disturbance. Rehabilitation of burned areas will not be successful when weeds can compete with native vegetation.

Can We Restore the Form and Function of Sagebrush Ecosystems?

Resource managers are faced with the question "What do we want this area to look like and can we achieve that goal?" Restoration of sagebrush ecosystems is limited by ecological and climatic dynamics that influence processes such as fire frequency, fire fuels, and rates of shrub regeneration. Financial costs for fire suppression and vegetation restoration, tempered by political concerns for use of our public rangelands, further complicate the issue.

We may need to accept that the future landscape dominating much of the Intermountain West will be an exotic annual grassland. Unlike old-growth forests that need only time, exotic annual grasslands may represent a habitat sink from which no alternative state is possible because of changes in soils, lack of seed sources for shrubs and perennial grasses, or frequent burning or disturbance (Westoby 1980). Using a computer simulation based on spatial and temporal dynamics of shrubland regeneration, we predicted that over a century of fire control, favorable climate, and optimum conditions for seed dispersal were required to replace the shrublands lost in just 20 years in the National Conservation Area (U.S. Dep. Inter. 1996). Even if restoration was a function of simply fire control and reseeding, the horizon is much longer than a typical resource management plan of 5 or 10 years. Existing fire rehabilitation programs provide only opportunities for a short-term response immediately following fires and not for the long-term support needed for restoration.

The perceived need to use nonnative plants to restore the form, even if the resulting function is unknown, further complicates restoration agendas. Native seed usually is expensive and often is available only in limited quantities compared to a more commercially feasible equivalent. However, I would rather invest our efforts into learning how to restore a functioning system with native components, even if initially constrained to small areas. Patchwork tinkering with cheaper, more readily available exotics, even if possible over larger areas, risks the consequences of yet another unknown commodity in the system. This "purist" philosophy carries a risk. We may not be at the bottom of the ecological barrel. New invasions of even more deleterious noxious perennial weeds could cause even greater ecological damage. If funding is an indication of the prevailing sentiment, only one United States federal program is devoted specifically to restoration of native vegetation in the Intermountain West despite the magnitude of the problem.

Finally, I will not ignore the impact of livestock grazing on future management directions. Although most of these lands never supported heavy grazing pressure, we continue to accommodate large domestic ungulates in our management and restoration plans. Restoration with native vegetation implies that a lower vegetation biomass will be available for grazing, that the ability to reseed overgrazed areas will be more costly, and that restrictions on livestock grazing will increase relative to use of nonnative species (grazing would not be allowed on seeded lands for a minimum of 5-8 years compared with 2 years for a crested wheatgrass seeding). These represent very real concerns to a livestock industry that has supported large-scale shrub eradication and reseeding with crested wheatgrass.

Consequences for the Loss of Sagebrush Ecosystems

The task of restoration is daunting and the outlook is discouraging because of the rapid deterioration of the system. Compared to the relative ease at which this ecosystem has changed and might still change into a system dominated by perennial noxious weeds, the cost and energy to return the system from a grassland-dominated state back to one dominated by a shrublands appears almost insurmountable. However, I think that the costs are even greater if the system remains in an exotic annual system from which we gain nothing and risk further deterioration from invasion of perennial noxious weeds.

Managers will not have the relative stability of a system dominated by native perennials because exotic annuals are more sensitive to climatic fluctuations. As a result, fires will be larger and more frequent, and costs for fire suppression and rangeland rehabilitation will be greater. The fire frequency on average for any place within the Snake River Birds of Prey National Conservation Area decreased from 80.5 years between 1950 to 1979 to 27.5 years from 1980 to 1994. For the National Conservation Area, an annual cost of $175,000 plus an initial expense of $650,000 will be needed to increase the control response and reduce fire size by 90% (U.S. Dep. Inter. 1995). We also can expect an increase in the current annual average of 90,000 ha of shrubsteppe that are burned each year and $10-15 million that are spent on fire fighting and rehabilitation in southern Idaho. In addition, the social cost can include loss of life for firefighters, property damage, and change in livelihood when traditional grazing lands are altered.

Loss of shrubs from these ecosystems is no less dramatic than clearcutting a forest. Managers now ask, "How much shrubland is enough?" The answer is complex, but like real estate, location is everything. A remnant shrub patch surrounded by large grasslands is less important than multiple shrub patches embedded within a larger mosaic of shrub and grasslands. Distribution and abundance of Brewer's (*Spizella breweri*) and sage sparrows (*Amphispiza belli*), having individual home ranges less than a hectare, are influenced by landscape configurations and habitat changes at scales greater than a kilometer (Knick and Rotenberry 1997, In press). Many other birds, such as sage grouse (*Centrocercus urophasianus*), associated with sagebrush habitats are undergoing significant population declines likely associated with local and large-scale loss of sagebrush and are listed as species at risk.

Requiem?

Documenting the changes from sagebrush to exotic annual grassland systems has been relatively easy. Turning that understanding into the solution is difficult and complex. However, we need to ask what we want our shrublands to look like and what we can achieve. Can we also accept that a full restoration will not be likely in our lifetime? I remain optimistic that we possess the capability to restore sagebrush ecosystems. But unless we develop an appreciation for an entire ecosystem, a large part of our landscape in the Intermountain West will sink into a different form and function in a relatively short time.

Acknowledgements

John Rotenberry and Jay Anderson are acknowledged for sharing their incredible insights into shrubsteppe ecosystems. Mike Pellant and Dave Pyke provided helpful comments on the manuscript.

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Editor's note. The Northwest Scientific Association has assisted the Tongass National Forest and the Pacific Northwest Research Station in obtaining independent (blind) technical reviews for various components of the science input to the Tongass Land Management Plan. A previous version of this manuscript was submitted to *Conservation Biology* in response to the article by Meffe et al. (1998) cited below, but was not accepted for publication by that journal.

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Independent Scientific Review in Natural Resources Management: A Recent Example from the Tongass Land Management Plan

The Society for Conservation Biology recently commissioned a paper on "Independent Scientific Review in Natural Resource Management" (Meffe et al. 1998). We read this publication with considerable interest, because our experience as scientists participating in development of the Land Management Plan for the Tongass National Forest (the largest national forest in the United States at 6.85 million hectares) led us to a similar conclusion over two years ago — there was a strong need for a rigorous evaluation of the use of scientific information in this highly controversial (Williams 1995) and still contentious (Durbin 1998) Land Management Plan (USDA Forest Service 1997). It is questionable if one could have found a more provocative land management situation to attempt such a scientific review. The Tongass has been a focus of often intense social, political, and ecological debate for over 40 years as this largely unaltered temperate rainforest contains abundant timber, wildlife, fish, mineral, and scenic resources in a unique archipelago setting.

We conducted our precedent-setting evaluation on the use of scientific information in the Tongass Land Management Plan over several months and prepared the final results in manuscript form. After an in-depth, independent scientific peer review, this manuscript was published (Everest et al. 1997). Our efforts also were presented in June 1997 at the annual meeting of the American Fisheries Society and in September 1997 in the Symposium on Advocacy in Science at the Wildlife Society Conference. Thus, published information specific to our effort on the Tongass National Forest, as well as other pertinent literature, was available to Meffe et al. (1998) to cite and discuss in their treatise. Curiously, they chose not to cite our widely distributed paper or any other well-known and available literature which, in our opinion, created a false impression regarding their originality.

As indicated by Meffe et al. (1998), there are several goals in conducting such a science- use review. We generally agree with their stated goals and consider that our evaluation of the Tongass Plan (Everest et al. 1997) accomplished the seven goals indicated in the commissioned paper, with the last three goals forming the basis of our approach. We provided another critical goal that is only alluded to by Meffe et al. (1998); that is, the review process should be designed to allow managers an opportunity to bring their developing policy direction in line with available scientific information. In this way, the review can serve to improve the final decision document rather than just deliver a report card on "how well did they do?" To accomplish this objective, the review process needs to be iterative; that is, it needs to be conducted coincident with development of the decision document and frequently shared with those making policy decisions (Fig. 1).

Our evaluation (Everest et al. 1997) of the Tongass Land Management Plan (USDA Forest Service 1997) went through several iterations as we shared drafts with managers for them to see "how they were doing" in various areas with regard to the application of available science information to policy development (Fig. 1). These subject areas included habitat for wildlife and fish,

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protection for caves and karst topography, slope stability, road management, various timber management issues, certain social and economic concerns, monitoring, and adaptive management. Policymakers frequently reconsidered management direction in these areas based on our review comments. They often changed direction in the emerging plan or added further clarification to acknowledge the nature of the available information bearing on the topic or the likely levels of risk (Shaw 1999) to one or more resources associated with the decision. For example, preliminary drafts of the Plan disallowed timber harvest within 150 meters of the beach to protect critical wildlife

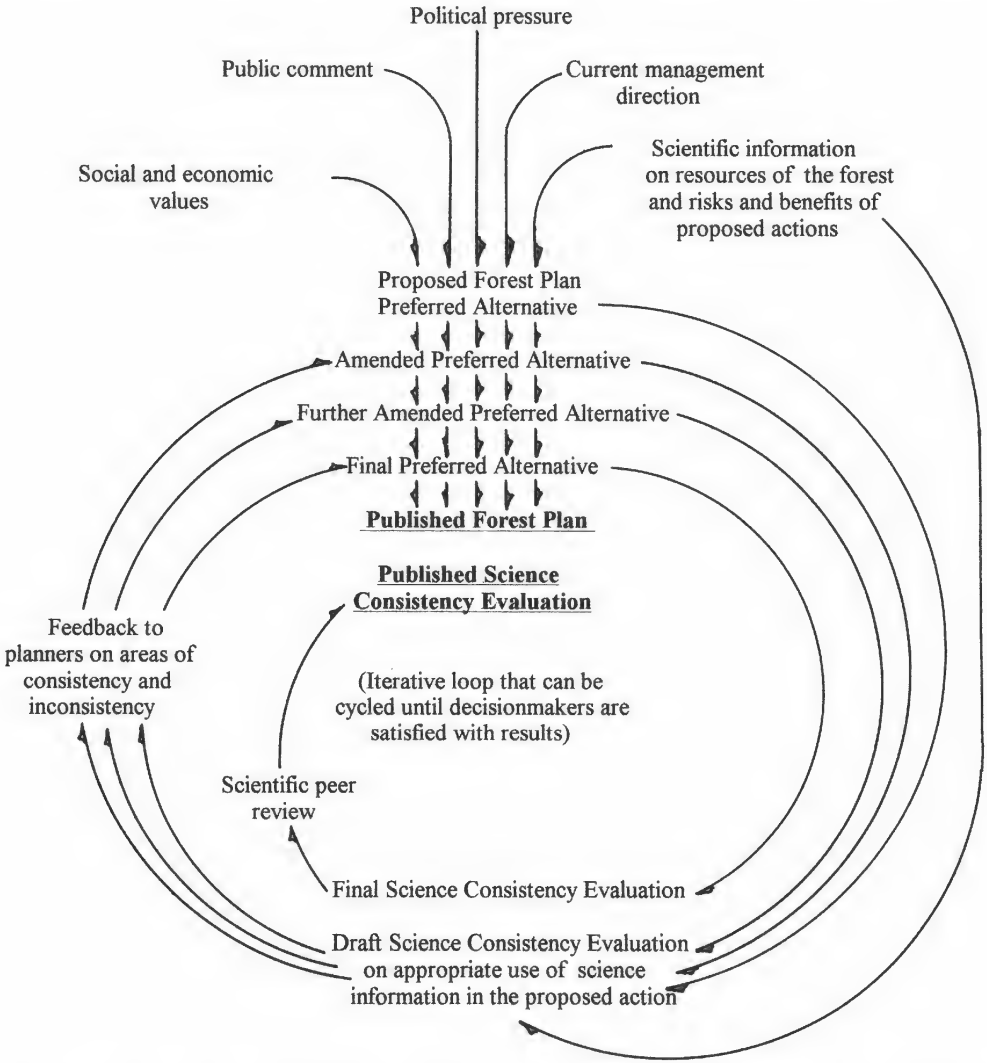
Political pressure
Public comment
Current management direction
Social and economic values
Scientific information on resources of the forest and risks and benefits of proposed actions
Proposed Forest Plan Preferred Alternative
Amended Preferred Alternative
Further Amended Preferred Alternative
Final Preferred Alternative
Published Forest Plan
Published Science Consistency Evaluation
Feedback to planners on areas of consistency and inconsistency
(Iterative loop that can be cycled until decisionmakers are satisfied with results)
Scientific peer review
Final Science Consistency Evaluation
Draft Science Consistency Evaluation on appropriate use of science information in the proposed action

Figure 1. Schematic diagram of the process used in developing the Tongass Land Management Plan. Without the addition of scientists to the team and their continued role in developing scientific information, interactively evaluating its use, and having their efforts peer reviewed by other scientists (left side of schematic diagram), it is questionable how well science-based information would have faired in the final plan.

habitat. Based on published information and risk assessment panels (Shaw 1999), our draft evaluation indicated that, in comparison to a 150- meter zone, a 300-meter zone markedly reduced risk to beach-adjacent wildlife habitat. In the final Plan, managers chose to reduce risk and disallowed timber harvest within a 300-meter zone; we (Everest et al. 1997) found this decision to be consistent with the available scientific information.

Another key component of a scientific review that Meffe et al. (1998) did not address is that decisionmakers need to have a clear understanding of the criteria that will be used by scientists to evaluate their proposed management policies. Forest plans and other land management decision documents often are criticized for having vague direction open to various interpretations; scientific reviews of such documents should not be open to similar criticism. Articulating in advance the criteria that will be used in the scientific evaluation alleviates this concern.

In the Tongass evaluation (Everest et al. 1997), we developed and applied the following criteria to address how scientific information was used by managers in setting policy:

- All scientific information made available to managers was considered in the decision.
- Scientific information was understood and correctly interpreted.
- Resource risks associated with decisions were acknowledged and documented.

All three criteria had to be met before a decision was considered to have appropriately used the available scientific information. Similarly, a management decision was considered to not have appropriately used available scientific information if any of the following circumstances occurred:

- Managers misrepresented or reinterpreted information in ways not supported by the original information.
- Managers selectively used information such that a different decision was reached than would have been made if all available information had been used.
- Decisions were stated and documented in such a way that implementation effects could not be predicted.
- Projected consequences of management actions were not consistent with scientific information.

In applying these criteria to the Tongass Land Management Plan, we concluded that the decisions made therein for riparian habitat, fish sustainability, wildlife viability, karst and caves protection, slope stability, timber resources, certain social and economic effects, and monitoring achieved a high degree of consistency with the available scientific information (Everest et al. 1997).

Through applying such criteria to management decision documents, it becomes apparent that certain contentious policy decisions are not necessarily inappropriate relative to available information just because some scientific reviewers may personally disagree with them. Although an essential consideration, science information does not "make" management decisions. Policymakers make such decisions after they complete what is essentially a value-oriented integration of the "positive and negative" features (environmental, economic, social, and political) of the projected outcomes of alternative management paths.

Because scientists using science information do not make management policy decisions, what part should scientists play in evaluating such decisions? It is our general position that scientists should not advocate, recommend, or impose any particular outcome or decision. To maintain neutrality and thus credibility, scientists should not impose their personal values into the process by making management recommendations. The personal values of scientists coupled with scientific information do not equal science. In this regard, four of the authors of Meffe et al. (1998) would have been poor choices for scientific review of the Tongass Forest Plan, because they signed a letter to the President of the United States advocating a particular management outcome on the Tongass.

In contrast to advocating any particular management direction, we contend scientists should advocate that the relevant scientific information be considered when a decision is made. They should, based on established criteria that are clearly articulated, determine when a decision has appropriately used the available science information and when it has not. Some further and contrasting discussions regarding the roles of scientists and managers in land management policy development appear in Philpot (1992) Risser and Lubchenco (1992), Hanley (1994), Lackey (1997), Lubchenco (1998), and Mills et al. (1998).

In the Tongass National Forest effort, we used an approach to conducting a science review somewhat different than that advocated by Meffe et al. (1998). We agree that independent scientific review of proposed management actions is of paramount importance, but today's natural resource issues on public lands involve a wide range of issues and the decisions surrounding these issues are extremely complex. This complexity requires that those reviewing the use of scientific information in management decisionmaking be fully aware of the relevant information base and be specifically acquainted with how it was used in developing and setting the policy.

Less than full knowledge could, even with the best of intentions, lead to a flawed review. It also could reduce the likelihood of, or extend the timeframe or mechanism for, achieving the necessary understanding, acceptance, and change by the management policymakers. We thus suggest a two-stage process in which the initial review is conducted by scientists who have followed the process and situation closely, or have in some way been *involved* with it so that they understand the various approaches and nuances used by managers in their policy setting. The independence of their review is established through the supervisory structure maintained in the planning effort (the scientists are not supervised by policy decisionmakers) and through the completed analysis being subjected to an independent, scientific peer review (Fig. 1).

In the Tongass effort, we were assigned to the planning team but reported to the Director of the Forest Service's Pacific Northwest Research Station rather than to the Alaska Regional Forester who approved the Land Management Plan. Administrative structure in the Forest Service is such that Directors of Research Stations are independent from Regional Foresters; their lines of authority meet only at the Forest Service Chief's office. Thus, the "authority separation" appropriately emphasized by Risser and Lubchenco (1992) as important for scientific involvement in land management policy formation was clearly maintained.

We were charged with developing a scientifically credible, value neutral-information base for the Tongass Land Management Plan, evaluating the quality of data and methods being used to develop the Plan, and clarifying the likely risks to various resources associated with alternative management scenarios (Mills et al. 1998). Finally, we independently conducted a science evaluation of the Plan which was itself subjected to a rigorous peer review and published (Everest et al. 1997). Thus, our approach followed the other primary guideline offered by Risser and Lubchenco (1992) for scientific involvement in land management policy formation. That is, to guard the scientific credibility of the effort [our evaluation], it must be subjected to the same kind of peer review that is expected in the process of conducting science.

The stated intent of the Alaska Regional Forester was to produce a scientifically credible and resource sustainable Land Management Plan for the Tongass National Forest. It became apparent that our involvement with development of the information base and independent review of the final product was essential to meeting that goal (Fig. 1). At times, our efforts and approach caused considerable consternation among management policymakers, particularly because they realized that our review would be published. They were not accustomed to having their decisions so closely scrutinized by Forest Service colleagues whom they did not manage. They also were unaccustomed to providing justification and acknowledgement of risks associated with their decisions. In the end, however, they did acknowledge that our involvement in the process and our insistence on maintaining independence from the management policy decisionmakers led them to incorporate the best available scientific information in the Forest Plan.

To our knowledge, this rigorous evaluation (Everest et al. 1997) of the way managers used scientific information in the Land Management Plan for the Tongass National Forest (USDA Forest Service 1997) is the first of its kind. We hope that others will build on the process we initiated and continue the debate stimulated by Meffe et al. (1998). We collectively should improve policy decision-making in management of public lands by ensuring rigorous review by qualified research specialists. The use of established criteria in a value-neutral manner will ensure that natural resource management is indeed science-based.

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Book Review

Conservation Biology Principles for Forested Landscapes

Joan Voller and Scott Harrison (editors). 1998. UBC Press, Vancouver. US$49.95 (clothbound, ISBN 0-7748-0630-3), US$29.95 (paperback, ISBN 0-7748-0629-X)

Conservation Biology Principles for Forested Landscapes is a great leap forward in the evolution of forest biology and management at large spatial scales in the Pacific Northwest and elsewhere. It is the single best book on this topic and deserves a spot on the bookshelf of everyone who studies and manages forest ecosystems.

The book maintains a high degree of clarity and objectivity throughout a broad range of topics. Eight chapters address the interaction of forest biology and management with respect to:

- Natural disturbance ecology (John Parminter)
- Spatial patterns in forested landscapes (Marvin Eng)
- Connectivity (Scott Harrison and Joan Voller)
- Riparian areas and wetlands (Joan Voller)
- Interior habitat (Angela von Sacken)
- Biodiversity and old-growth forests (Andy MacKinnon)
- The dead wood cycle (Eric Lofroth)
- Managing for edge effects (Joan Voller)

While this is not a comprehensive list of issues in forest conservation biology, it covers most of the relevant ecological and managerial issues of the past decade. These topics are addressed in a remarkably evenhanded manner, without the eco-jargon and value-laden descriptions found in much of the conservation biology literature. Wherever potentially ambiguous terminology is used—fragmentation, natural variability, matrix, etc.—definitions are provided to guide subsequent discussion.

Another distinctive feature of the book is a focus on forest ecosystems of British Columbia (BC), with compilation of the book being led by the Centre for Applied Conservation Biology at the University of British Columbia. While the authors draw on all of the rich literature on forest ecosystem science in the Pacific Northwest, most of the examples are from BC forests. The many citations from BC studies will broaden the perspectives of readers from the United States who are accustomed to literature focused on Washington and Oregon. Although the concepts covered by these BC authors are generally the same as those covered in other volumes dominated by U.S. authors, the entirety of the message is decidedly more coherent and less biased.

Conservation Biology Principles contains a number of outstanding contributions. The chapter on natural disturbance by Parminter is the very best discussion I have seen on this topic and should be required reading for forest ecology students. This chapter employs a spatio-temporal framework, including a historical perspective and clear examples at different spatial scales. There is an excellent list of specific ways in which natural processes can be incorporated more directly in resource management.

Similarly the chapter on spatial patterns in forested landscapes by Eng is an excellent summary of both concepts and the effects of human activities on patterns. As the author points out, "many terms [in landscape ecology] are simply nothing but pedantic jargon." He then dedicates an entire page to definitions of commonly used terms in landscape ecology, and even lists the spatial scale of *landscape*, the first time I have seen this overused and much abused term so explicitly defined. Subsequent discussion focuses on the effects of forest fragmentation on spatial patterns and a wide range of ecosystem processes. The chapter concludes with an interesting summary of how strategic forest management activities can be used to create various patterns. Definitions, concepts, ecological patterns, and management applications are all concisely discussed in this chapter.

The remaining chapters are packed with information and examples. The chapter on biodiversity and old-growth forests by MacKinnon is a bit of an outlier, because it is focused mostly

on summaries of plants and animals associated with late-successional forests. However, the extensive lists of plant and animal taxa (including the less charismatic ones) and exhaustive literature citations make this chapter a primary reference for information on old-growth biota.

I must include a few negatives amidst the compliments. *Conservation Biology Principles* desperately needs a synthesis chapter at the end. If there is another edition of the book, I would encourage the editors to provide not only some summary perspectives of the preceding chapters, but a vision for the future of forest conservation biology. There is also considerable overlap between some of the chapters, and while the completeness of individual chapters makes them better standalone products, I found the redundancy annoying when reading the book from cover to cover. Finally, many of the photographs—presumably black-and-white photos derived from color slides—are of poor quality (at least in my paperbound copy) and therefore provide little additional impact to the concepts discussed in the text. This is another item that could be cleaned up in a subsequent edition.

Despite these glitches in editing and production, the material contained in the book spans an impressive array of ecological information applied to the management of forest ecosystems. It is written in an engaging style accessible to both scientists and students, and provides a common base of knowledge with which all forest resource managers should be familiar. I predict that *Conservation Biology Principles for Forested Landscapes* will become a classic in the forest biology literature. If readers take these principles to heart, the result will be improved management of forestlands in the Pacific Northwest.

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Northwest Science
Volume 72 (1998)
Author and Subject Index

AUTHOR entry headings are distinguished from subject entry headings by capitalization. The two special issues of *Northwest Science* published in 1998 are each identified by a prefix: S1 (for the forest fire issue) and S2 (for the British Columbia coastal forests issue).

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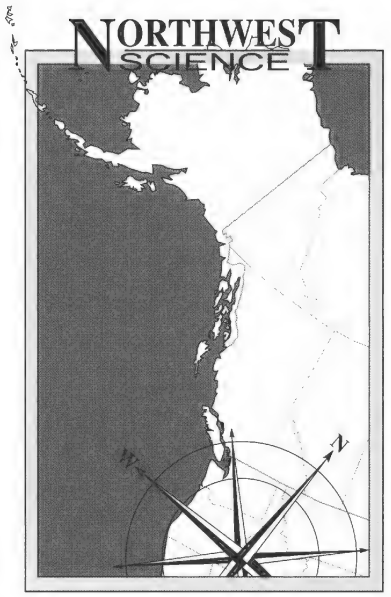

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Quarterly Publication of the Northwest Scientific Association

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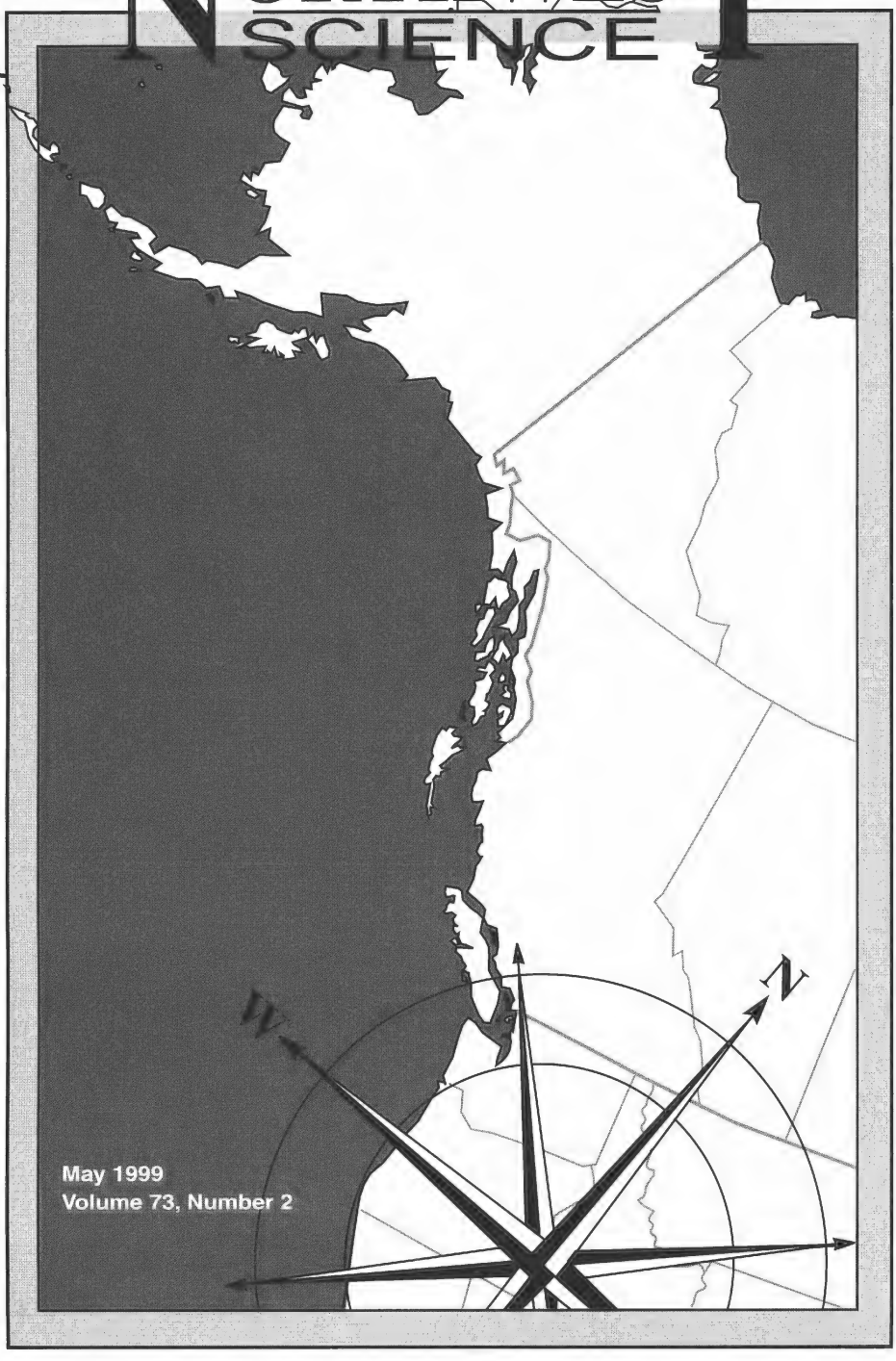

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ISSN #0029-344X

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Announcements

Honorary Life Member Award

Robert L. Edmonds is this year's recipient of the Honorary Life Member Award. Dr. Edmonds has been a member of Northwest Scientific Association (NWSA) since 1975. He regularly attends the annual meeting and has been a spark at introducing graduate students to NWSA. He has been the *Northwest Science* Associate Editor for Soils since 1990. The Honorary Life Member award was presented to Dr. Edmonds in recognition of his contributions and service to the Association.

Originally from Australia, he completed his Ph.D. in Forest Pathology at the University of Washington in 1971. He immediately became a member of the faculty as a Research Associate in the College of Forest Resources (CFR), University of Washington. He advanced to Assistant Professor in 1976 and became a full Professor in 1982. He was Chair, Ecosystem Science and Conservation Division at CFR from 1993 to 1997. His research and teaching interests have spanned a broad range of disciplines from pathology to interdisciplinary studies of forest ecosystems. His major interests include pathology (root diseases); the below-ground ecosystem; aerobiology and the effects of air pollution; the chemistry of precipitation and streams; and forest ecology. He has published more than 150 scientific papers and has edited one book: *Analysis of Coniferous Forest Ecosystems in western North America*; a new book co-authored with James Agee and Robert Gara, *Forest Health and Protection,* is to be published in the year 2000. His current teaching load includes Forest and Society, Forest Pathology, Forest Protection, Soil Microbiology, and Forest Ecosystems. He enjoys hiking in the Cascades and Olympic Mountains, and spending his time traveling throughout North America, and in his native homeland, Australia.

Outstanding Scientist Award

During an era of intense focus on wildlife conservation in the context of broader perspectives on ecosystem management, **Dr. Douglas B. Houston** has been at the forefront of wildlife science. His contributions to ungulate biology and a wide range of high-profile resource management issues have left a lasting mark on public lands in the Pacific Northwest and beyond.

Doug Houston set a prescient tone for natural resource science with his article "Ecosystems of National Parks," which appeared in *Science* in 1971. This was at a time when people were only beginning to discuss "ecosystem science" and public agencies were not yet tuned into science-based resource management. It was a wake-up call for the National Park Service and other agencies to adopt a new management paradigm that allowed for the functional dynamics of flora and fauna at large spatial and temporal scales. The concept of "ecosystem management" was not popularized until the late 1980's, but Houston set forth some of the fundamental concepts in his seminal paper.

Most of Doug Houston's work is typified by meticulous, detailed study of organisms and systems over time. He is perhaps best known for his work on ungulate ecology, starting in the 1960's with studies of moose and predator-prey interactions in Grand Teton National Park. Over the course of the next decade, he became the leading national authority on elk, culminating in the publication of his landmark book *The Northern Yellowstone Elk: Ecology and Management*. His data and perspectives on the ecology of elk are a cornerstone of the scientific foundation for wildlife management in Yellowstone.

After transferring to Olympic National Park in 1980, Doug Houston continued his studies of elk, and began studies on yet another controversial wildlife issue, the management of mountain goats on the Olympic Peninsula. Houston became a leading authority on this species while working with a team of scientists to study the effects of this alien ungulate on alpine ecosystems. His careful work on mountain goat biology over the course of a decade resulted in the monograph *Mountain Goats in Olympic National Park: Biology and Management of an Introduced Species* and enabled resource managers to understand the population dynamics of the goats, thereby providing critical input to management decisions.

In 1989-90, Doug Houston was appointed to serve on the Interagency Committee for the Conservation of the Northern Spotted Owl, in recognition of his ability to translate wildlife population data into large-scale management applications. He helped write the landmark Conservation Plan that changed the way forest resources are managed in the Pacific Northwest.

Doug Houston has made several other notable contributions. He initiated a study of the ecological role of salmon in aquatic and terrestrial ecosystems, finding that salmon carcasses are a food source for a wide range of terrestrial species. This is now common knowledge, but he was the first to quantify the phenomenon. Although now retired from active research, Houston has an important new book on *Yellowstone and the Biology of Time*, a photographic retrospective of the changing landscape over more than a century in Yellowstone National Park (See review in this issue of *Northwest Science*). He is currently at work on yet another monograph, this one dealing with Roosevelt elk on the Olympic Peninsula.

A career federal scientist, Doug Houston has always been a strong advocate of applied science, and his contributions to wildlife ecology have had a profound impact on the management of wildlife on public lands. He is not a promoter of his own work and has not engaged in advocacy, preferring to let his data and publications speak for him. Doug Houston has contributed significantly to the evolution of modern wildlife science. His professional record and scientific integrity over a 35-year professional career truly make him worthy of the NWSA Outstanding Scientist award.

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Distribution and Abundance of *Neotoma* in Western Oregon and Washington

Abstract

Bushy-tailed woodrats (*Neotoma cinerea*) and dusky-footed woodrats (*N. fuscipes*) add substantially to the prey base of many avian and mammalian predators. High biomass of woodrats can reduce markedly area requirements of predators; thus, management for woodrats has potential in conservation. But patterns of abundance of woodrats in the Pacific Northwest are poorly understood. Our objective was to determine local abundances and regional distributions of *N. cinerea* and *N. fuscipes* in forests west of the Crest of the Cascade Range in Oregon and Washington.

We sampled a variety of forests from 1985 to 1997 in seven physiographic provinces. In Washington, we found that *N. cinerea* was rare in upland forests, but abundant along rocky streams on the eastern Olympic Peninsula and in rock bluffs on the west slope of the Cascade Range; *N. fuscipes* does not occur in Washington. In Oregon, *N. fuscipes* is at the northern limits of its range and we found that it was rare in Douglas-fir (*Pseudotsuga menziesii*)-western hemlock (*Tsuga heterophylla*) forests; *N. cinerea* was common in old forests and along streams. In mixed-conifer forests both species occasionally were abundant, but their abundances were negatively correlated. *Neotoma cinerea* was rare in mixed-conifer-mixed-evergreen forests but *N. fuscipes* occasionally was abundant in early, and present in late stages of forest development. The distribution of *N. fuscipes* can be explained by its preference for dense shrub cover and it ability to consume plants potentially toxic to other mammals; the only compelling explanation for the irregular distribution of *N. cinerea* is exceptional vulnerability to predation because of its size and social behavior.

Because of zoogeographic restrictions, limited opportunities exist in western Oregon and Washington to manage habitat for woodrats as a means of assisting in the recovery and maintenance of viable populations of predators sensitive to loss or management of forests.

Introduction

Pacific Northwest forests are inhabited by a variety of small mammals (Ruggiero et al. 1991, Carey 1995, Carey and Johnson 1995). They occupy diverse niches in forest communities and intermediate positions in trophic pathways, providing the nutritional foundation for many of the vertebrate predators in forest ecosystems (Carey et al. 1992, 1996). Of particular interest in forest ecosystem management are the larger small mammals (28-280 g), which tend to be arboreal or semi-arboreal (Carey 1991, 1996). These rodents are preferred prey for predators including coyotes (*Canis latrans*), foxes (*Vulpes vulpes* and *V. velox*), bobcats (*Lynx rufus*), weasels and skunks (Carnivora: Mustelidae), hawks and other birds of prey (Falconiformes), and owls (Strigiformes) (*see* Ingles 1965, Maser et al. 1981, and Carey 1991 for overviews or Carey et al. 1992, Carey and Kershner 1996, Wilson and Carey 1996, and Watson et al. 1998 for specific examples). The largest of these small mammals, the dusky-footed woodrat (*Neotoma fuscipes*) and the bushy-tailed woodrat (*N. cinereus*), are especially attractive to predators (Linsdale and Tevis 1951, Escherich 1981, Carraway and Verts 1991, Carey and Peeler 1995, Sakai and Noon 1997) and measures of spotted owl (*Strix occidentalis*) fitness can be related to abundance of woodrats (Carey et al. 1992, Carey and Peeler 1995). The bushy-tailed woodrat has a broad geographic distribution, encompassing the entire Pacific Northwest, whereas the dusky-footed woodrat inhabits northern California, southwestern Oregon, and the Willamette Valley (Hall 1981). Woodrats are more limited in local distribution and abundance in the forests of western Washington and western Oregon than other small mammals, despite their large size and ability to use low quality foods (Escherich 1981, Carey et al. 1992).

Here we provide empirical data on body mass, sex ratios, abundance, habitats, and distribution of *Neotoma* that we gained from cross-sectional live-trapping surveys of habitat types throughout

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the Pacific Northwest and develop hypotheses about mechanisms underlying patterns of woodrat abundance based on a synthesis of our results and the scientific literature.

Study Areas

Vegetation Zones

Our study spanned three vegetation zones, the Western Hemlock Zone, the Mixed-Conifer Zone, and the Mixed-Conifer/Mixed-Evergreen Zone (Franklin and Dyrness 1973). The Western Hemlock Zone encompasses much of low to mid-elevation western Washington and western Oregon. As we use the term, the Mixed-Conifer Zone includes the coniferous forest vegetation at the margins of interior valleys in southwestern Oregon (Figure 1). These valleys <152 m in elevation were described by Bailey (1936) as Upper Sonoran Life Zone-warm, dry areas that are phytologically an extension of northern California flora and markedly different from most of western Oregon and Washington, for example, in having grass, shrubs, and oaks (*Quercus* spp.) as

Figure 1. Woodrat (*Neotoma*) study area locations in Washington and Oregon west of the Cascade crest, 1985-1997; physiographic provinces adapted from Franklin and Dyrness (1973); black dots approximate study area locations within provinces; the Southern Washington Cascades were not sampled.

dominant natural vegetation. Mixed-Conifer Zone forests and Upper Sonoran grasslands and oak woodlands occur along the Umpqua and Rogue river valleys north and south of Roseburg, Oregon, respectively (Bailey 1936, Franklin and Dyrness 1973). The upland forests of southwestern Oregon provide the transition between the Western Hemlock Zone (north of latitude 43^0 N, e.g., Roseburg) and the Mixed-Conifer-Mixed-Evergreen Zone (south of 43^0 N).

Boundaries between vegetation zones were not distinct and forest vegetation did not necessarily correspond strictly to mapped zone boundaries. In areas of moderate relief, the transition was a continuum; in areas of sharp changes in aspect or elevation, changes in plant communities were marked. Vegetation zones did not coincide with zoogeographic regions or physiographic provinces. For example, the Columbia River is a zoogeographic barrier separating the Western Cascades of Oregon and the Southern Washington Cascades, but is spanned by the Western Hemlock Zone (Franklin and Dyrness 1973, Ruggiero et al. 1991). Yet, each province within Washington comprised parts of more than one vegetation zone. No zoogeographic barriers separated the vegetation zones of southwestern Oregon. Rather, there were biogeographic ecotones between zones. Composition of wildlife communities varies with both vegetation association and physiographic province and differences in species of wildlife associated with various forest communities in various physiographic provinces were specified by Bailey (1936), Ingles (1965), Maser et al. (1981), Brown (1985), and Ruggiero et al. (1991).

Physiographic Regions

Study areas were in seven physiographic provinces (Table 1, Figure 1) west of the Crest of the Cascade Range in Washington and Oregon (Franklin and Dyrness 1973): Northern Cascades, Olympic Peninsula, and Puget Trough in Washington and southern Western Cascades, southern Coast Ranges, Klamath Mountains, and Interior Valleys (hereafter referred to more specifically as the Umpqua Valley) in Oregon. These areas differed markedly in climate, landform, and vegetation, some of which formed zoogeographic barriers for small mammals (e.g., major features such as mountains, rivers, grasslands) and all of which interacted to shape the fauna and flora of each province (Ruggiero et al. 1991).

In each province, both old-growth and second-growth forests were sampled. Riparian areas were sampled on the Olympic Peninsula and in southwestern Oregon. Special landscape features (ridge tops, talus slopes, rock outcrops, and stream-side deciduous forests) were sampled in southwestern Oregon. We located large study areas in each physiographic province. Within study areas we selected stands (areas of homogeneous forest vegetation >10 ha; e.g. Tables 1 and 2) or sites (special landscape features that often were linear in shape-ridges and streams or small in size <7 ha; e.g. Table 3). We chose stands representative of the most abundant seral stages in the study area and classified them on the basis of vegetation zone, seral stage, and management history (i.e., arising from natural disturbance (natural) or those arising from clearcutting (managed)). Management history was important because stands originating after clearcutting usually have substantially fewer biological legacies (such as large snags and large fallen trees) than stands originating after catastrophic wildfires or windstorms and may follow a different trajectory of ecosystem development than natural stands. Natural stands often differ in structure, composition, and function from managed stands (Ruggiero et al. 1991; Carey 1995, 1998; Carey and Johnson 1995; Carey et al. 1999).

Seral Stages

Seral stages of forest ecosystem development and stages of timber stand development (e.g., clearcut, sapling, pole, sawlog) are not equivalent and stand age is only moderately correlated with each type of development (Carey and Curtis 1996, Carey 1998). For this study, natural stands were old forest (>80 yr) with some stands >200-yr old (old growth). Managed stands were <80-yr old. We used six of the eight stages of forest development from the ecosystem classification of Carey and Curtis (1996) to categorize our study stands and sites; the strength of that classification is that it incorporates effects of management history and natural disturbance. The stages we used were (1) old growth, >200-yr old with very large trees, diverse species composition, understory development, and high coarse woody debris loads; (2) niche diversification, 80-200-yr old with developed understory and abundant coarse woody debris but structures (trees, snags, logs, canopy height) of smaller stature than old growth; (3) developed understory, >40-yr old, with high foliage height

TABLE 1. Study areas, seral stages, number of stands, years, trappings sessions, nights trapped, and captures and mean densities (number/ha) of bushy-tailed woodrats (*Neotoma cinerea*) in upland and stream-side forests in the Northern Cascades, Olympic Peninsula, and Puget Trough of Washington and Western Cascades, Coast Ranges, Umpqua Valley, and Klamath Mountains of Oregon, 1985-1997.

Province & locations	Seral stage[a]	Stands (*n*)	Years & periods (*n*)	Trap nights (*n*)	Captures (*n*)	Density(*n/ha*)
Northern Cascades			**1991-1996**			
Baker Lake	O	3	2	8,480	0	
Darrington	C	2	2	6,400	0	
Olympic Peninsula			**1987-1989**			
Eastern	N/U	2	2	6,400	0	
Southcentral	O/U/C	6	1-3	25,600	0	
Western	O/N/C	6	2-3	22,400	0	
			1989			
Eastern riparian	O/N	6	1	6,400	44	0.9
Eastern upland	N	6	1	6,400	6	0.1
Puget Trough			**1991-1997**			
Ft. Lewis	U/C	16	11	180,224	0	
Lewis and Clark	0	1	3	3,072	0	
Capitol Forest	N	1	4	4,096	0	
Western Cascades			**1993-1996**			
Diamond Lake 1	N	6	4	20,664	1	<0.1
North Umpqua	O	6	2	5,576	28	0.2
Cottage Grove	U	6	2	11,120	3	<0.1
Diamond Lake 2	U	6	1	2,520	1	<0.1
Coast Ranges			**1985-1989**			
Roseburg-Coos	O/N	6	3-8	48,576	18	<0.1
Bay-Drain	U/C	5	2-6	16,992	6	<0.1
Umpqua Valley			**1985-1989**			
North of Roseburg	O/N	3	2-7	26,560	71	0.4
	C	4	4-5	21,632	0	
Klamath Mountains			**1988-1989**			
South of Roseburg	O	2	2	8,000	1	<0.1

[a] Seral stage codes: old growth (O), niche diversification (N), understory reinitiation (U), competitive exclusion (C).

TABLE 2. Frequency of capture (*F*) of bushy-tailed woodrats (*Neotoma cinerea*, NECI) by number of sampling sessions (*S*) and in relation to the number of dusky-footed woodrats (*N. fuscipes*, NEFU) in old and young stands trapped intensively with grids of traps by physiographic province and vegetation zone (Western Hemlock, WHZ; Mixed-Evergreen-Mixed-Conifer, MEZ; the transition zone between the two; and the Mixed-Conifer Zone, MCZ).

	Natural old stands (>80 yr)			Managed stands (35-80 yr)		
Province-vegetation type	Stands (*n*)	S_{NECI} (S_{TOTAL})	F_{NECI} (F_{NEFU})	Stands (*n*)	S_{NECI} (S_{TOTAL})	F_{NECI} (F_{NEFU})
North Cascades-WHZ	3	0 (6)	0 (0)	2	0 (4)	0 (0)
Olympic Peninsula-WHZ	7	0 (20)	0 (0)	7	0 (13)	0 (0)
Puget Trough-WHZ	2	0 (7)	0 (0)	16	0 (176)	0 (0)
Coast Ranges-transition	6	8 (29)	16 (1)	4	4 (20)	5 (0)
Western Cascades-transition	12	10 (34)	29 (1)	4	2 (10)	3 (0)
Umpqua Valley-MCZ	3	15 (15)	101 (26)	4	0 (18)	0 (0)
Klamath Mountains-MEZ	2	1 (3)	1 (27)			

TABLE 3. Density (numbers/ha) of bushy-tailed woodrats (*Neotoma cinerea*, NECI) and dusky-footed woodrats (*N. fuscipes*, NEFU) and number of stick nests recorded in a survey of special landscape elements in southwestern Oregon, 1987-1988.

Stand name	S[a]	Zone- prov.[b]	NECI (*n*)	NEFU (*n*)	Nests (*n*)	Landscape element-habitat features
Rader	O	WH-CR	0.7 (4)	0	0	Stream side, boulders, log jams
Folley	O	WH-CR	0	0	0	Ridge top, talus
Look	O	WH-CR	0	0	0	Ridge top
Wood	O	MC-IV	0	0.5 (2)	2	10% rock cover; intermittent stream
Canyon	O	MC-IV	0	0.8 (3)	2	intermittent stream
Turkey	O	MC-KM	0.2 (1)	0.2 (1)	4	talus
Darby	O	MC-KM	0	2.0 (8)	0	
Wolf2	N	WH-CR	0.7 (4)	0	0	stream side Douglas-fir, bigleaf maple
Wolf3	N	WH-CR	0.3 (2)	0	0	stream side, red alder, bigleaf maple
Cougar	N	WH-CR	0.2 (1)	0	0	stream side, bigleaf maple, red alder
Hubb	N	MC-IV	0.7 (4)	0	0	90% rock outcrops
Doe	N	MC-IV	0	0	0	ridge top
Yello1	N	MC-IV	0.7 (4)	0	0	stream side, boulders, red alder
Yello2	N	MC-IV	1.3 (8)	0	4	stream side, red alder, bigleaf maple
Case	D	WH-CR	0	0	1	stream side, red alder
Camas	D	WH-CR	0	0.2 (1)	6	stream side Douglas-fir, red alder
Bottle	D	MC-IV	0.2 (1)	4.2 (17)	6	stream side Douglas-fir, red alder
O'Shea	D	MC-KM	0	2.0 (8)	9	15% influenced by stream
Tyee	C	MC-IV	0.8 (5)	0	0	2 intermittent streams
Camp	C	MC-IV	0	1.8 (7)	7	small Douglas-fir
Wood	C	MC-IV	0.5 (3)	1.0 (4)	5	small Douglas-fir
Gravel	C	MC-KM	0.2 (1)	0.2 (1)	6	25% stream influence
Cany1	I	MC-IV	0	3.2 (13)	9	intermittent stream, boulder, debris
Cany2	I	MC-IV	0.3 (2)	1.2 (5)	5	Douglas-fir
Cany3	I	MC-IV	0	0	4	25% influenced by stream, boulders
Lost	I	MC-IV	0.2 (1)	0	2	intermittent stream, red alder, grass
Garden	I	MC-IV	0	0	2	int. stream, Douglas-fir, boulders

[a] Seral stages: old growth (O), niche diversification (N), developed understory (D), understory reinitiation (U), competitive exclusion (C), ecosystem initiation (I).

[b] Zones: Western Hemlock Zone (WH), Mixed-Conifer-Mixed-Evergreen (MC); physiographic provinces: Coast Ranges (CR), Interior Valley (IV), Klamath Mountains (KM).

diversity including shade-tolerant trees, but with little coarse woody debris; (4) understory reinitiation, 30-200-yr old with developed low shrub layers and a shade-tolerant understory absent or just starting to form; (5) competitive exclusion, 30-200-yr old, densely stocked with trees, closed canopy, little understory; and (6) ecosystem initiation, 0-30-yr old, which includes grass, forb, shrub, and open sapling stages.

Specific Study Areas

Northern Cascades of Washington: Stands were between 365 and 610 m elevation with average annual precipitation of 250 cm and mean minimum January temperatures of -2.5^0 C. The old-growth vegetation type was western hemlock, swordfern (*Polystichum munitum*), and three-leaved foamflower (*Tiarella trifoliata*). Competitive-exclusion stands were dominated by Douglas-fir and salal (*Gaultheria shallon*).

Olympic Peninsula of Washington: For upland stands, elevations ranged from 85 to 610 m, average annual precipitation ranged from 130 to 200 cm on the eastern sites to >300 cm on the south-central and western sites, and minimum January temperatures averaged 0^0 C. Old- growth and

niche-diversification stands were wet to mesic, dominated by western hemlock with associates of silver fir (*Abies amabilis*), Sitka spruce (*Picea sitchensis*), or Douglas-fir. Competitive-exclusion and understory-reinitiation stands were in the same rainfall zones as the old stands, but were mesic to dry vegetation types—western hemlock, western hemlock and Douglas-fir, or Douglas-fir with understories dominated by moss, Oregon oxalis (*Oxalis oregona*), or salal. Paired riparian and upland sites on the eastern Olympic Peninsula were dominated by Douglas-fir averaging 38-118 cm dbh, with associates of western redcedar (*Thuja plicata*), western hemlock, and silver fir with understories of Pacific yew (*Taxus brevifolia*), and bigleaf maple (*Acer macrophyllum*).

Puget Trough of Washington: Stands were at 100-160 m elevation with 80-cm annual precipitation and January lows of 0 to 2.5^0 C. Competitive-exclusion stands were dominated by 55-yr-old Douglas-fir with sparse understories of salal and Cascade Oregongrape (*Berberis nervosa*). Understory-reinitiation stands were dominated by 65-yr-old Douglas-fir with abundant salal, California hazel (*Corylus cornuta*), and swordfern. The niche-diversification stand was a mixture of mature (>90 yr) bigleaf maple with Douglas-fir, western redcedar, western hemlock and red alder (*Alnus rubra*). The old-growth stand had superdominant Douglas-fir, dominant western redcedar, midstory bigleaf maple and vine maple (*Acer circinatum*), and an understory of deciduous shrubs.

Southwestern Oregon: In the southern Coast Ranges, stands were 79-488 m in elevation, received 100-160 cm precipitation, and had low temperatures of 0^0 C. Umpqua Valley margins were 290-457 m in elevation, received 60-80 cm precipitation, and had lows of 0 to 2.5^0. Stands in the Klamath Mountains were 390-610 m in elevation, received 80 cm precipitation, and had lows of 0^0 C. Old-growth stands ranged from Douglas-fir/western hemlock/western redcedar (300-400 yr) to Douglas-fir/grand fir (*Abies grandis*)/incense-cedar (*Libocedrus decurrens*), 275-350-yr old. Umpqua-Valley-margin stands variously had true oaks *(Quercus* spp.), poison-oak (*Rhus diversiloba*), and other vegetation typical of the Mixed-Conifer Zone. Tanoak (*Lithocarpus densiflorus*) and pines (*Pinus ponderosa* and *P. lambertiana*) were common in stands in the Klamath Mountains. Both old-growth stands in the Klamath Mountains were estimated to have dominant trees 210-yr old; Iron had an 80-yr old midstory, whereas O'Shea had two age classes (60 yr and 90 yr) in its midstory. Younger forests were dominated by Douglas-fir and salal with some having evergreen hardwoods (e.g., *Castanopsis chrysophylla* and *Arbutus menziesii*).

In the southern Western Cascades, the Diamond Lake study areas were at the juncture of the Western Hemlock Zone and White Fir (*Abies concolor*) Zone, 945-1,707 m in elevation, with 80-120 cm precipitation, and minimum temperatures of -2.5 to -5.0^0 C. Niche-diversification stands were Douglas-fir, white fir, western hemlock, and Shasta red fir (*Abies magnifica*), 110-130-yr old. Some salvage logging had been done in the 1970s. Commercially thinned understory-reinitiation stands were composed of Douglas-fir, white fir, and incense-cedar, 165-yr old, with light understories of white fir and little coarse woody debris. North Umpqua old-growth stands were at the juncture of the Western Hemlock Zone and Mixed-Conifer/Mixed-Evergreen Zone, wet with seeps and streams, 1,219-1,402 m in elevation, with overstories of Douglas-fir, white fir, western hemlock, and western white pine (*Pinus monticola*) 200-520-yr old, and understories of vine maple and Cascade Oregongrape. Cottage Grove understory-reinitiation stands were at the juncture of the Western Cascades and the Interior Valley (Willamette River Valley) Provinces, in the Mixed-Conifer Zone. These stands were 488-792 m in elevation and had seeps and streams, overstories of Douglas-fir 60-80-yr old, 2-5 old-growth trees/ha, and understories of Pacific rhododendron (*Rhododendron macrophyllum*), salal, vine maple, and Cascade Oregongrape.

Finally, we studied 27 sites in the Coast Ranges-Umpqua Valley margins-Klamath Mountains that represented particular elements of landform (ridge tops, riparian areas, areas of exposed rock, boulders, or talus) and early (<40 yr) seral stages. These landscape elements were linear in arrangement, small in area, or patches disjunct from like environments.

Methods

Experimental Design

Our study was exploratory and covered wide areas, but sample sites were not selected randomly from all sites within the range of each species. In some areas, all accessible sites were sampled.

In others, samples of common seral stages of forest development were selected preferentially and considered representative of those seral stages in that area. There could be unknown biases in our site selection (for example, preconceived notions of what constitutes "representative" old growth or "typical" managed forests) and there certainly are confounding factors (both biotic and abiotic) that make isolation of causal factors impossible. Practically any category of forest condition we developed was heterogeneous—it could be broken down into finer categories. These limitations are common to almost all field studies; yet, despite violations of assumptions, most field studies use inferential statistics (Cook and Campbell 1979, Hoaglin et al. 1991). Nevertheless, we conducted no statistical tests and present only descriptive statistics and rank correlations. We thereby make it clear that our conclusions are inferences and deductions based on non-statistical assumptions, empirical data, and published reports. Thus, our conclusions should be viewed as hypotheses.

Sampling

We followed the methods developed by Carey et al. (1991a) for sampling populations of arboreal and semi-arboreal rodents, including woodrats. We used Tomahawk 201 single-door, collapsible box traps constructed of 16-gauge galvanized wire mesh (1.3 by 2.5-cm mesh size), 13-cm wide, 13-cm tall, and 41-cm long and baited with peanut butter and oats. We placed traps either in grids with 40 m between grid points or just on the ground in paired lines of traps 20-m apart (Carey et al. 1991a). We sampled woodrat populations in forest stands with grids of traps, with equal numbers of traps in trees and on the ground. Traps were placed 1.4-m high on the largest tree within 5 m of a trap station; traps on the ground were placed at locations <5 m from the trap station where captures would be most likely (e.g., near dens, travel ways, under shrubs, or along fallen trees). Grid size varied from 7 by 9 (10 ha) with 1 trap/station (Western Cascades) to 8 by 8 (10 ha) with 2 traps/station (Puget Trough), to 10 by 10 (16 ha, with some exceptions) with 2 traps/station (Northern Cascades, Olympic Peninsula, Coast Ranges, Umpqua Valley margins, and Klamath Mountains); traps were opened for 8 nights. We studied woodrats at the sites of special landscape features (including stream-sides on the Olympic Peninsula) with parallel trap lines of 25 stations (2 traps/station on the ground) each (a total of 100 traps); traps were opened for 3-4 nights. We assumed the areas sampled by trap lines were 4 ha for dusky-footed woodrats and 6 ha for bushy-tailed woodrats as suggested by Carey et al. (1991a, 1992), who based their estimates on mean maximum distances moved between subsequent recaptures during grid trapping. We used numbers of individuals caught per trapping session (minimum number known alive, MNKA) as a measure of the size of the local population or social group. We converted individuals to density by dividing by the effective area sampled. For both arboreal and semi-arboreal sciurids, individuals caught per unit effort and MNKA are highly correlated with each other and with mark and recapture population estimates across a wide range of population densities and linear regression coefficients are similar among physiographic provinces in the Pacific Northwest; total captures per unit effort are poorer predictors of population size than captures of individual animals (Carey et al. 1991a, 1999; Carey *in press* a, b). We assumed MNKA estimates of population size of semi-arboreal woodrats were as valid as those for sciurids. These estimates slightly underestimate population size. We also assumed density is a measure of carrying capacity and provides an index to habitat quality (Carey *in press* a, b). We recorded numbers of stick nests in the areas sampled only in the Coast Ranges-Umpqua Valley margins-Klamath Mountains studies. Sex and body mass of woodrats were recorded in the Olympic riparian and Coast Ranges-Umpqua Valley margins-Klamath Mountains studies.

Although sampling effort varied among stands and between stands and sites, large efforts were expended at each stand. Even at our small sites (<7 ha) of special landscape features we trapped for 300-400 trap nights; trap success was higher at the sites than at stands, suggesting a poor correlation between trapping effort and captures at the levels at which we trapped. Carey et al. (1991a) and others report the ease of capture for woodrats. For example, Escherich (1981) reported that 85% of bushy-tailed woodrats were caught in the first night of trapping and recommended that the number of individuals caught be used as a measure of abundance and not catch per unit effort of trapping. Catch per unit effort could produce misleading results with animals patchily distributed

in small social groups of three to four individuals (like bushy-tailed woodrats) because the longer, more intensively, and larger an area was trapped the lower the population estimate would be. Our experience was similar to that of Carey et al. (1991a) and Escherich (1981)—when we caught woodrats we caught them quickly; when we didn't catch them quickly additional trap nights did not result in greater success. We caution the reader, however, that one can not demonstrate absence with this sort of sampling, only low probability of occurrence; abundance is more easily demonstrated. Laudenslayer and Fargo (1997), moreover, reported difficulty trapping dusky-footed woodrats at 2.2-ha sites in California oak woodlands (2 captures/100 trap nights) except at woodrat houses (10-13 captures/100 trap nights), suggesting probability of capture of woodrats with traps in grids may be low in some vegetation types. With densities and conditions comparable to those studied by Laudenslayer and Fargo (1997), however, using our methods, we would still statistically expect to catch a minimum of 6-8 woodrats per site.

Results

We caught 196 individual bushy-tailed woodrats and 124 dusky-footed woodrats in 199 sampling sessions at 119 sampling locations (Table 4; 93 surveys of stands, Table 1, and 27 surveys of special habitat types, Table 3, with overlap on 1 site; ca. 500,000 trap nights).

Bushy-tailed Woodrats

Bushy-tailed woodrats were not captured in upland forests in the Northern Cascades, Puget Trough, or Olympic Peninsula except in unmanaged, upland forests immediately adjacent to stream-side forest on the eastern Olympic Peninsula. These stream-side forests, however, had the highest average densities of bushy-tailed woodrats of any sites we sampled in Oregon or Washington (Tables 1 and 3)—0.9 woodrats/ha (averaged over six sites). Here, bushy-tailed woodrats had a sex ratio (males: females) of 1:1.3 (10 sessions with 40 woodrats captured). Density in two occupied riparian areas averaged 1.8 woodrats/ha (9-12 woodrats/location) with 0.2-0.3 woodrats/ha (1-2 woodrats/location) in the adjacent uplands; however, another riparian area had 0.3 woodrats/ha (2 woodrats) and three riparian areas had none.

In the southern terminus of the Western Hemlock Zone in Oregon, bushy-tailed woodrats commonly were found in stream-side, natural Douglas-fir/western hemlock forests (niche diversification and old growth, four of four stands) and in upland, mid-slope forests (three of six old-growth stands and three of four second-growth stands), but were absent from two ridge-top, old-growth stands and two managed, stream-side stands with developed understories. As in Washington, the adjacency of streams was not sufficient to ensure occupancy of forests by bushy-tailed woodrats. Average densities were low (Table 1). Over time, occupancy of individual stands was variable, averaging 27% of trapping sessions in old, natural stands and 20% in managed stands (Table 2), suggesting frequent, local (stand-level) extinctions. Overall, bushy-tailed woodrats exhibited a similar pattern of abundance and variable occupancy in the Western Cascades (Table 2).

In contrast to the Washington samples, Oregon Coast Ranges-Umpqua Valley margins-Klamath Mountains samples had skewed sex ratios of 1:2.3 (135 woodrats caught in 43 sessions, averaging 3.1 woodrats/location), significantly different from a 1:1 ratio ($P < 0.05$). Average densities were low and ranged from <0.1/ha to 0.4/ha, depending on habitat type (Table 1). The highest density

TABLE 4. Percent frequency of occurrence of bushy-tailed woodrats (*Neotoma cinerea*, NECI) and dusky-footed woodrats (*N. fuscipes*, NEFU) in old, natural stands and young, managed stands with and without permanent streams in western Washington and western Oregon; only mixed-conifer and mixed-conifer/mixed-evergreen stands (*n* in parentheses) were counted for occurrence of NEFU.

	Stream present			Stream not present			Total		
Age	Stands (*n*)	NECI (%)	NEFU (%)	Stands (*n*)	NECI (%)	NEFU (%)	Stands (*n*)	NECI (%)	NEFU (%)
Old	27 (1)	78	100	34 (8)	21	63	61 (9)	46	67
Young	12 (4)	33	75	46 (11)	17	45	58 (15)	20	53
Total	39 (5)	64	80	80 (19)	19	53	119 (24)	34	58

recorded was 1.3/ha (3 male and 5 female bushy-tailed woodrats) in a stream-side red alder/bigleaf maple stand. Male bushy-tailed woodrats had a body mass ($\bar{x} \pm$ SE) of 276 ± 10 g (n = 27); females weighed 255 ± 6 g (n = 47). We found 55% of female bushy-tailed woodrats to be lactating or just post-lactating from 1 May to 15 November.

Dusky-footed Woodrats

Dusky-footed woodrats were not caught in Washington. Only two dusky-footed woodrats were caught in Douglas-fir-western hemlock forests in Oregon despite intensive trapping (Tables 2 and 3); one in a niche-diversification stand at 366 m elevation and one in a stream-side developed-understory stand at 488 m elevation; both in the Coast Ranges. Densities of dusky-footed woodrats in occupied mixed-conifer and mixed-conifer-mixed-evergreen stands ranged from 0.1/ha to 4.3/ha ($\bar{x}$ = 1.2 ± 0.3/ha). Dusky-footed woodrats were caught in two of six managed, low-elevation, mixed-conifer, understory-reinitiation stands in the Western Cascades (Cottage Grove). Male dusky-footed woodrats had a mean mass of 288 ± 9 g (n = 29); females weighed 225 ± 10 g (n = 25), on average; sex ratio was 1:1.2 (123 woodrats caught in 22 sessions, $\bar{x}$ = 5.6 woodrats/location). Seventy-four percent of female dusky-footed woodrats were lactating or post-lactating during 16 May-31 October.

Sympatric Woodrats

Both bushy-tailed woodrats and dusky-footed woodrats were more common in the mixed-conifer forests of the Umpqua Valley margins (Tables 1, 2, 3) than in the southern Douglas-fir-western hemlock forests of the Coast Ranges or Western Cascades. Bushy-tailed woodrats were abundant (0.2-1.3/ha) in, but occasionally absent from, late-seral and stream-side stands. In intensively trapped stands, occupancy in old, natural stands and absence from managed stands 35-80-yr old were constant (Table 2). Dusky-footed woodrats were abundant (0.2-0.8/ha) in all but one old-growth stand, in one of three niche-diversification stands (0.1/ha), and especially in one stream-side developed-understory stand (4.3/ha) that also had bushy-tailed woodrats (0.2/ha). Dusky-footed woodrats were found in all but one of the stands sampled in the Klamath Mountains; compared to dusky-footed woodrats, bushy-tailed woodrats were rare in the Klamath Mountains (Tables 2 and 3). The two species were found together in five of eight mixed-conifer old-growth stands, three of six mixed-conifer competitive-exclusion stands, and in one mixed-conifer stream-side stand. Within these sites, abundances of the two species were negatively correlated (Spearman rank correlation = -0.52, $P < 0.05$).

Overall, relative frequencies (percent of sites with woodrat captures, Table 4) suggest that optimum habitat for bushy-tailed woodrats was old, natural forests (>two-fold margin) with streams (almost a four-fold margin). Dusky-footed woodrats were 1.5 times more frequent near streams, but only slightly (1.3 times) more likely to occupy old, natural forest than young, managed forests (mostly 40-90-yr old).

When we caught woodrats in southern Oregon, we caught more dusky-footed woodrats, on average, than bushy-tailed woodrats. The sex ratio of bushy-tailed woodrats was skewed towards females; dusky-footed males and females were equally common. More female dusky-footed woodrats had borne young than had female bushy-tailed woodrats. The two species did not differ significantly in weight. Biomass of dusky-footed woodrats (1,548 g/ha) was greater, on average, than that of bushy-tailed woodrats (876 g/ha). Abundances of the two species were negatively correlated (Spearman rank correlation = -0.52, $P < 0.05$).

Stick nests, or woodrat houses, were readily apparent in all but one stand (mixed-conifer old growth) where dusky-footed woodrats were captured. Dusky-footed woodrats took shelter in these nests when released. However, the numbers of stick nests and the numbers of dusky-footed woodrats captured were not correlated (Spearman rank correlation = 0.47, n = 15, P = 0.08). Total numbers of woodrats (both species) were correlated with number of nests (Spearman rank correlation = 0.39, n = 27, P = 0.049). Bushy-tailed woodrats, however, sought shelter in cavities in trees, under logs, or in rock crevices when released from traps. Few nests were present where only bushy-tailed woodrats were caught and many nests were present when both species were caught.

Discussion

Woodrats in Western Washington

Dusky-footed woodrats were absent, as expected (Ingles 1965, Hall 1981), and bushy-tailed woodrats were unexpectedly rare (given range descriptions by Ingles 1965, Hall 1981, and Brown 1985) in upland Douglas-fir-western hemlock forests in Washington. We found bushy-tailed woodrats only on the relatively dry, eastern Olympic Peninsula, near some streams. The streams with woodrats were narrow, deeply cut, and associated with forested boulder fields. The streams without woodrats did not have nearby boulder fields, talus, or rock outcrops. Some of our upland stands elsewhere on the Peninsula had small streams nearby or within them, too small to have changed the upland nature of the forest or the landform, but no woodrats. Thus, the mere presence of water within a forest was not sufficient for habitation by bushy-tailed woodrats. Additional trapping (4,162 trap nights with Tomahawk 201 traps) in oak (*Quercus garryana)* woodlands and Douglas-fir forest-prairie ecotones in the Puget Trough found no woodrats (Ryan and Carey 1995). The restricted distribution we observed was far more narrow than the broad distribution across stages of forest development and vegetation zones suggested by Ingles (1965) or Brown (1985).

Dalquest (1948) described bushy-tailed woodrats in Washington as inhabiting buildings in the mountains with natural habitat of broken rock or talus from sea level to 3,048 m (on Mt. Rainier in the Southern Washington Cascades). He stated only one or two woodrats would be found at a given locality. His distribution map shows bushy-tailed woodrats at Forks, Quinault, and Quilcene, the vicinities in which we trapped on the Olympic Peninsula. Locations we trapped had little or no broken rock or talus, except for some stream-side areas on the eastern Olympic Peninsula, where we did catch woodrats. There, in stream-side boulder fields, we caught 9-12 woodrats per site (1.5-2.0/ha) and single woodrats in the uplands. These were greater concentrations than the small, scattered groups of one to four and sex ratios were not skewed towards females as is usually reported (Dixon 1919, Dalquest 1948, Escherich 1981). Our stream-side sites, however, were larger (>4 ha) and more continuous than the discrete rock outcrops studied by others. Spotted owls actively foraged in our occupied study areas and their diets included woodrats (E. D. Forsman, pers. comm. 1989; Forsman et al. 1991). Thus, even when bushy-tailed woodrats were not broadly distributed, they were sought out and preyed upon by spotted owls.

Holmes (1995) set traps for bushy-tailed woodrats in a rock bluff (150 m high and 900 m wide) at 500-650 m elevation above Rattlesnake Lake in the Southern Washington Cascades physiographic province near North Bend, Washington and caught 22, 20, and 16 woodrats in 1992, 1993, and 1994, respectively, about 1.5/ha, on average. Woodrats denned in the rock cliffs and foraged in nearby forest. Adult sex ratios (1:4, 1:2.3, 1:0.9, respectively) were skewed towards females in two of three years. Charles R. Knox (pers. comm., 1997) removed, sequentially over four years, three woodrats from his cabin at the juncture of a stream and the Greenwater River (elevation 550 m) in the Southern Washington Cascades in an area of wet forests and rock bluffs. Lawrence L. C. Jones (pers. comm., 1989), while trapping *Martes americana*, occasionally caught woodrats in rock outcrops, talus slopes, and log piles at high elevations near tree line in the Southern Washington Cascades just north of Mt. Rainier. Thus, we can confirm Dalquest's (1948) description of the distribution and habitat of the bushy-tailed woodrat in Washington, but not his conclusions that only one or two woodrats would be found in a single locality. The number of woodrats present seems more to reflect the area of contiguous denning habitat (rock or talus) than the social behavior of the species.

The association of bushy-tailed woodrats with rock outcrops was also reported in the Canadian Rocky Mountains where it was found that competition for scarce den sites (crevices in rock) resulted in agonistic behavior toward non-kin and stable, cohesive relationships within family groups (Moses and Millar 1992). Far to the south, Dixon (1919) found bushy-tailed woodrats were confined to high elevations in northern and eastern California and almost exclusively associated with cliffs, boulder piles, rock slides, and logs. He thought that use of rock crevices was beneficial in protection from snow storms and predators. Local distribution, however, was irregular. Not all rock slides were occupied. There was rarely more than a family of five or six individuals in a rock slide of 1-2 ha; average density was <0.1/ha. Similarly, Escherich (1981) found woodrats living in groups

of one adult male and one to three adult females. Escherich (1981) also reported that the most important resource for the bushy-tailed woodrat was adequate rock shelter for protection from snow and cold; he thought shelter was more limiting than food. Escherich (1981) suggested that much bushy-tailed woodrat biology is adapted to exploiting limited rock outcrops as secure denning sites. In particular, he cited small social groups, polygyny, and sexual dimorphism in body mass as adaptations to exploiting limiting, patchy resources (rock outcrops). In our few occupied areas in Washington, we observed larger groups without sex ratios indicative of polygyny. Our data from Oregon supports small social groups and polygyny, with sex ratios skewed towards females, but the 95% confidence intervals for male and female body mass overlapped completely.

Woodrats in Western Oregon

Bailey (1936) reported that bushy-tailed woodrats were found throughout the forests of western Oregon, primarily in cliffs and masses of broken rock. Maser et al. (1981) also reported the affinity for rock, but stated bushy-tailed woodrats were found throughout coniferous and deciduous forests and denned in hollow trees where rock was scarce. Doyle (1985, 1990) found bushy-tailed woodrats, but no dusky-footed woodrats, in old-growth forests along streams (0.2 ± 0.1/ha) and in adjacent uplands (0.2 ± 0.1 ha) in the Western Hemlock Zone in the central Western Cascades near Blue River, Oregon (north of our Western Cascade study areas). However, in the same general vicinity, Anthony et al. (1987), in a similar comparison of stream-sides and uplands, and Rosenberg (1990), in an intensive comparison of managed and old-growth stands, did not report capturing any woodrats. Cudmore (1986) found bushy-tailed woodrats in talus, rock outcrops, and under bridges near Blue River. Neither he nor Gilbert and Allwine (1991) reported finding bushy-tailed woodrats in their extensive small mammal studies in young, mature, and old-growth upland forests near Hood River in the northern Western Cascades or in the central Western Cascades.

We caught bushy-tailed woodrats in abundance (1) in one old-growth area in the southern Western Cascades (North Umpqua, a flat area of pumice soil with six sites averaging 0.2 woodrats/ha; three sites had 0.3-0.7 woodrats/ha, three sites had 0.1-0.2 woodrats/ha), (2) in old forests in the Umpqua River Valley margins (0.4 woodrats/ha; level to moderate slopes, small streams, one site with rock outcrops), (3) along streams in the valley margins and Coast Ranges, and (4) in one area of rock outcrop in a valley margin. Two streams had boulders associated with them. In general, however, it was difficult to find areas of talus, rock outcrops, or boulders in our southwestern Oregon study areas.

We sampled our old-forest, valley-margin, mixed-conifer sites 2-7 times 4-6 months apart and caught bushy-tailed woodrats each trapping session. Abundances were lower in Douglas-fir transition forests and repeated sampling showed habitat occupancy was variable over time (8 of 29 sampling sessions). It appeared that bushy-tailed woodrats were absent from many upland sites and underwent periodic local extinctions in their habitats in the Douglas-fir transition forests but not in the valley-margin mixed-conifer forests. Local extirpations due to predation also were observed by Escherich (1981) in the California Sierra Nevada. He attributed this phenomenon to the harem social structure of the bushy-tailed woodrat, which results in clumping of the small population and concomitant attraction of predators. Both species of woodrats were important prey of the spotted owl in our Oregon study areas and owls actively foraged in most of the old forest sites and many of the stream-side sites occupied by woodrats in the Coast Ranges, Interior Valleys, and Klamath Mountains (Carey et al. 1992, Carey and Peeler 1995).

Several factors may have been important in determining patterns of occurrence of bushy-tailed woodrats in upland and stream-side forests without rock shelters in southwestern Oregon and absence from such areas elsewhere. Prey biomass and diversity was higher than in Douglas-fir-western hemlock forests to the north (Carey et al. 1992). Abundance in Douglas-fir transition forests was lower than in interior-valley mixed-conifer forests and mixed-conifer-mixed-evergreen forests to the south. As prey biomass available to the spotted owl decreased northward, predation pressure on bushy-tailed woodrats may have increased. Similarly, predation pressure on bushy-tailed woodrats may have been more intense in transition forests than in mixed-conifer forests. Whereas northern flying squirrels (*Glaucomys sabrinus*) and bushy-tailed woodrats were the common prey in transition forests, they and dusky-

footed woodrats, brush rabbits (*Sylvilagus bachmani)*, and red tree voles (*Phenacomys longicaudus*) were abundant and were common prey in mixed-conifer and mixed-conifer-mixed-evergreen forests (Forsman et al. 1984, 1991; Carraway and Verts 1991; Gillesberg and Carey 1991; Carey et al. 1992). Multiple, abundant prey species allow spotted owls to use small home ranges (Carey et al. 1992) and may dilute predation pressure on any single species (or cause owls and other predators to focus on the most abundant and concentrated prey, the dusky-footed woodrat). In southern Oregon transition forests, intensive predation by spotted owls appeared to reduce dense populations of northern flying squirrels by 50% and locally extirpate bushy-tailed woodrats (Carey et al. 1992). In a dense population of dusky-footed woodrats in northern California mixed-conifer-mixed-evergreen forest, predators killed 50% of juveniles and 30% of adults (Sakai and Noon 1997). Indeed, the large number of larger small mammals that serve as prey for strigids and mustelids and the presence of stick houses of dusky-footed woodrats (potential den sites for various prey species, including bushy-tailed woodrats) may have facilitated the occurrence of the bushy-tailed woodrat in forest without rock shelters (*see* Carraway and Verts 1991 for a list of species commensal with dusky-footed woodrats).

The climate of interior valleys is warm and dry; rock shelters are not necessary for protection from cold temperatures and rain nor are rock areas necessary for subnivean travel and storage of food for overwinter use as is necessary in areas of heavy snowfall. Bushy-tailed woodrats build their own stick houses (on the ground) and stick nests (in trees) in southwestern Oregon (Maser 1965, 1966; Maser et al. 1981; Carey 1991). Bushy-tailed woodrats also use cavities in trees extensively (Carey 1991, Carey et al. 1997; Maguire, unpublished data). With multiple species (northern flying squirrels; both species of woodrat; Douglas'squirrels, *Tamiasciurus douglasii*; western gray squirrels, *Sciurus griseus*; and red tree voles) using stick nests, tree cavities, and fallen trees as shelter (Maser et al. 1981; Carey 1991, 1996; Carraway and Verts 1991; Gillesberg and Carey 1991; Carey et al. 1997), competition for dens could be strong. Bushy-tailed woodrats are territorial and interspecifically aggressive. One of us (ABC) observed a male bushy-tailed woodrat kill one female dusky-footed woodrat and one female northern flying squirrel in a 1.2 by 1.2 by 2.4-m cage with a surplus of food and nest boxes. Thus, bushy-tailed woodrats may have been more common in old forest than managed competitive-exclusion stage forest because understory vegetation, fallen trees, and cavities in standing trees were more abundant in old forests than young, managed forest (Carey 1995; Carey et al. 1991b, 1997, 1999). In northern forests, cavities are less abundant (Carey et al. 1997), rainfall is higher and cool temperatures are more common, and we did not find stick nests built by bushy-tailed woodrats. Ground fires are less frequent than in southern forests, thus fewer hollow trees form as a result of fire scars. Abundances of cavities and hollow trees may be too low to allow bushy-tailed woodrats to locate clustered housing for one to five woodrats central to one or more patches of abundant food. If clusters of cavities were found, travel to arboreal dens without the dilution effect of multiple prey species could make woodrats especially vulnerable to predation by owls. Dens in standing and fallen trees often do not have multiple entrances and exits and ability of long-tailed weasels (*Mustela frenata*) to prey on cavity-nesting mammals may be enhanced (Wilson and Carey 1996, Carey et al. 1997).

Abundance along streams may have been due to increased abundance of deciduous trees (*Alnus rubra* and *Acer macrophyllum*) and undergrowth and accumulation of coarse woody debris near streams, especially in very young and old forests. Colonization of stream-side areas in old forest by early successional species is common because of dense shrubby vegetation (Carey 1988). Stream noise can interfere with the ability of owls to detect prey by sound at night and might provide woodrats with some protection from predation. Neither the bushy-tailed woodrat nor the dusky-footed woodrat are particularly efficient at water conservation— both benefit from the availability of free water (Meserve 1974, Carraway and Verts 1991) .

Abundances of the two species of woodrats were negatively correlated in mixed-conifer forests and bushy-tailed woodrats were rare in mixed-conifer-mixed-evergreen forests in the Klamath Mountains where dusky-footed woodrats were increasingly abundant. Bailey (1936) reported that dusky-footed woodrats could be found throughout the Upper Sonoran Life Zone (interior valleys and their margins) and the mixed-conifer

and mixed-conifer-mixed evergreen forests of southwestern Oregon, particularly in shrub lands and areas of dense underbrush in forests; Maser et al. (1981) reiterated this distribution. Cudmore (1986) and Gilbert and Allwine (1991) caught dusky-footed woodrats (1 each) in the southern Western Cascades. Hooven (1959) reported that dusky-footed woodrats could achieve densities of 0.2-0.7/ha in dense Douglas-fir thickets. We trapped dusky-footed woodrats on 15 occupied sites; density ranged from 0.1/ha to 4.3/ha, averaging 1.2 ± 0.3/ha. Densities of dusky-footed woodrats increases in mixed-conifer-mixed-evergreen forests and dusky-footed woodrats may be abundant enough there to exclude bushy-tailed woodrats. Densities reported for dusky-footed woodrats in California ranged from 5/ha to 45/ha (Carraway and Verts 1991). Sakai and Noon (1997), however, reported densities as high as 81/ha in ecosystem initiation stages of mixed-conifer-mixed-evergreen forests in northern California.

Dusky-footed woodrats build their own houses and can live in large colonies; they seem to be limited more by food, water, and vegetative cover than by housing sites. In California, Raphael (1988), Ward (1990), and Sakai and Noon (1993, 1997) all found dusky-footed woodrats most abundant in early seral stages, with a secondary peak of abundance in a bimodal distribution in late-seral stages; none found bushy-tailed woodrats in their studies. One of us (CCM), however, did catch bushy-tailed woodrats in 350-yr old growth along a stream in Trinity County, California. The low densities and marginal environments we found in southwestern Oregon may reflect decreased habitat quality for dusky-footed woodrats at the northern limits of its range in upland forests. Low densities may explain the lack of correlation between numbers of stick houses and numbers of dusky-footed woodrats given the high correlations reported by Sakai and Noon (1993, 1997). However, Cranford (1977), Wallen (1982), and Lynch et al. (1994) did not report high correspondence between number of houses and number of individuals either.

Hard-leaved sclerophylls become increasingly less common the farther north of California (Franklin and Dyrness 1973). These plants, especially tanoak and other evergreen hardwood trees and shrubs can become extremely abundant in clearcuts (and even delay development of coniferous forest) in California. In stable, stream-side, alder (*Alnus*)/willow (*Salix*) and chaparral environments, dusky-footed woodrats colonies may persist >25 yr (Linsdale and Tevis 1951, Wallen 1982). In old forests, with canopy gaps and histories of frequent fires that produced open canopies, patchy but stable areas of brushy understories develop and provide habitat for dusky-footed woodrats. Dense, evergreen vegetation <3 m can provide food, cover, and travel ways for dusky-footed woodrats. Woodrat diets often reflect local feeding specializations, but dusky-footed woodrats are particularly specialized (Atsatt and Ingram 1983). A series of adaptations allows dusky-footed woodrats to feed on evergreen leaves high in fiber, tannins, and phenolics. These include (1) digestive tract microflora that help maintain the woodrat's nitrogen balance, (2) reingestion of feces, (3) large, insulated houses that decrease energy expenditure, (4) location of houses near preferred food plants to decrease travel time and exposure to predators, (5) hoarding food that not only permits continuous, high volume feeding but also helps detoxify the food through enzymatic breakdown and release of toxic chemicals. In summary, dusky-footed woodrats appear limited by stable, densely brushy environments for food and cover from predation, materials for housing construction, dispersal ability, and climate. In mixed-conifer-mixed-evergreen forests both brush fields (chaparral; early, open stages of evergreen hardwood forests; and coniferous forests with well-developed sclerophyllous understories) and densely vegetated stream-sides provide stable, high quality environments. Stability and density of vegetation structure may be more important than vegetation composition. Dusky-footed woodrats are habitat specialists, which despite adaptations to high fiber, tannins, and phenolics, often exhibit generalized food habits (Meserve 1974). In mixed-conifer and transition forests, moderate to poor quality habitat for both dusky-footed woodrats and bushy-tailed woodrats can be found along streams and in some old-growth forests. In Western Hemlock Zone forests, there is no habitat for dusky-footed woodrats, and bushy-tailed woodrats are generally relegated to rocky areas and high elevations, along with some other larger small mammals (e.g., *Marmota* spp., *Ochotona princeps*, *Spermophilus saturatus*).

Hypotheses and Implications for Conservation

Our research suggests that woodrats are limited in distribution and abundance in southern Oregon forests because the highest quality habitat for dusky-footed woodrats—dense, shrubby, early stages of forest development—is scattered over large landscapes dominated by competitive-exclusion forest and is relatively ephemeral, suitable as habitat for only 5-10 yr. Competitive-exclusion forests may persist 30 yr under intensive management for timber and up to 200 yr without timber harvests. Colonizing potential habitat created by clearcutting thus requires hospitable intervening habitat, aggressive dispersal behavior, or well developed dispersal corridors. Old-growth forests with patches of dense cover provide moderate quality habitat. We hypothesize that the abundance of dusky-footed woodrats over a landscape could be increased by landscape-level management that includes variable-density thinning, in managed stands, that is designed to mimic spatial patterns characteristic of old-growth and niche-diversification forests (Carey and Curtis 1996). This hypothesis can be tested in adaptive management experiments at the landscape scale, with treatment units of small watersheds. Carey and Curtis (1996) provide guidance for multiple-objective management for biodiversity that is also appropriate for woodrats. Strategies include variable-density thinning combined with coarse woody debris management and creation of debris piles from thinning slash, management of stream side areas to restore coarse woody debris and complex vegetation structure, and management of mass-wasting areas to promote recruitment to streams of coarse woody debris and coarse rocky debris at failure. Treatments are designed to (1) allow colonization of managed forests by both woodrat species, (2) facilitate colonization through maintenance of sources of colonizers, i.e., populations along streams, and (3) contribute to a larger, more viable metapopulation in the landscape.

Our review suggests that lack of clusters of den sites in upland forests with developed understories and without rock outcrops limits the distribution of bushy-tailed woodrats in Washington by making occupancy impossible in some instances and allowing only small populations susceptible to extirpation by predation in other cases. Even abundant, scattered coarse woody debris is insufficient to allow woodrats to occupy old-growth forests in western Washington (Carey 1995, Carey and Johnson 1995). This hypothesis could be tested via experiments in which large piles of debris could be constructed from thinning operations designed to enhance understory development. These experiments should be conducted within reasonable distances (e.g., < 1 km) of occupied woodrat habitat and cover large enough areas (ca. 6-10 ha) to be true tests of the hypothesis.

Acknowledgements

Thanks to those that participated in the various studies especially those with lead roles, including B. Casler, A. Center, S. Center, C. Chambers, J. Feen, A. Gillesberg, J. Lehmkuhl, T. Manning, P. Reed, and W. McComb. We thank W. Laudenslayer, H. Sakai, P. Ward, J. Waters, and S. Wilson for their careful reviews of draft manuscripts. Support for this paper was received from the USDA National Research Initiative and Forest Service (Pacific Northwest Research Station, Olympic National Forest, Umpqua National Forest), the Roseburg District and Oregon State Office of the Bureau of Land Management, Oregon State University, and the U. S. Army, Fort Lewis. Use of product names in this report was for information only and does not imply an endorsement by the U. S. Department of Agriculture.

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Received 19 March 1998
Accepted 9 April 1999

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Classification of Species Attributes for Pacific Northwest Freshwater Fishes

Abstract

Fish assemblages integrate physical and chemical habitat conditions and are used to evaluate the condition of water resources in the Pacific Northwest. To facilitate such evaluations, we classified each of the 132 freshwater fish species known to occur in the Pacific Northwest (Idaho, Oregon, Washington) by its origin, overall pollution tolerance, adult habitat, adult feeding, and water temperature preference. Recommendations from regional fishery experts, published literature, and the aggregate experience of the authors were used to classify species. The attribute classifications were responsive to human disturbance of aquatic habitats when applied to fish assemblages sampled from throughout the region. Our attribute classification of fish species promotes use of fish assemblages to evaluate water resource conditions regionally and fosters greater acceptance of biological measures of water resource quality.

Introduction

The use of fish assemblages for assessing water quality is in response to mandates of the Clean Water Act (Water Environment Federation 1997) requiring States to restore and maintain biological integrity. The U.S. Environmental Protection Agency (USEPA) recommends that States do this by developing narrative and numeric biological criteria (USEPA 1990, Gibson 1996). To date, northwestern states have developed only narrative biological criteria. For example, in the vast majority of streams in the Pacific Northwest, state statutes call for protection of "beneficial uses" of water, such as salmonid spawning, cold water biota, or no detrimental changes in biological communities (Idaho Department of Health and Welfare 1993, Oregon Secretary of State 1998, Washington Administrative Code 1997). Previously, however, not all freshwater fish species of the Pacific Northwest were classified by metrics commonly found useful for quantitatively evaluating attainment of beneficial uses and biological integrity (e.g., as described by Yoder and Rankin 1998). In addition, there were inconsistent metric classifications for the same species in drainages shared by multiple states, hindering interstate assessments and regional collaboration. Because of high public and economic interest in these resources, USEPA support for quantitative biocriteria, and the interstate ranges of many of the fish species, there is clearly a need to develop more effective assessment tools to evaluate Pacific Northwest water bodies using their fish assemblages.

Fish assemblages have proven useful to describe and assess biological condition of specific waters in the Pacific Northwest (Hughes and Gammon 1987, Fisher 1989, Friesen and Ward 1996, Maret et al. 1997, Hughes et al. 1998). This is because fish are integrators of water resource conditions, and information about their structure and function may be used to assess these conditions (Li et al. 1987). Specifically, fish assemblages are useful in evaluating biotic integrity, defined as "the ability of an aquatic ecosystem to support and maintain a balanced, integrated, adaptive community of organisms having a species composition comparable to that of the natural habitats within a region" (Frey 1977, Karr and Dudley 1981).

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According to Karr et al. (1986), the capability of fish assemblages to accurately reflect environmental quality lies in their integration of five major factors that determine the condition of a water resource. These factors include hydrology, water quality, biological interactions, physical habitat structure, and energy resources. Because fish assemblages integrate these characteristics of their environments, they are useful for evaluating the effects of human activities on particular sites or across entire regions (Karr 1981).

Assessments of biotic integrity have typically included classes of attributes or metrics describing species richness, species composition, trophic structure, fish abundance, and fish condition (Miller et al. 1988, Hughes and Noss 1992, Simon and Lyons 1995, Simon 1998). Each metric reflects the quality of a different aspect of the fish assemblage that responds in a different manner to aquatic ecosystem stressors. The index of biotic integrity (IBI), first formulated by Karr (1981), combines these metrics into an index of water resource condition. Recent applications summarized in Simon (1998) have shown that the IBI concept is widely adaptable, but metrics must be modified, deleted, or added to reflect regional differences in fish distribution and assemblage structure.

Fish assemblage attributes such as origin (native or alien), overall tolerance to pollution, habitat and temperature preferences, and trophic structure have been found responsive to human disturbance (Hughes and Gammon 1987, Simon and Lyons 1995, Karr and Chu 1999) and useful in evaluating biotic integrity (Miller et al. 1988, Chandler et al. 1993, Yoder and Rankin 1998). Human disturbance can increase taxa richness in cold water streams (Lyons et al. 1996, Maret 1997) as cool and warm water species invade where water temperature regimes have been altered by such activities as agriculture, logging and urban development. Highly altered aquatic habitats are particularly vulnerable to invasion by alien (introduced, non-native, exotic) species (Moyle and Nichols 1973, Holden and Stalnaker 1975, Leidy and Fiedler 1985, Moyle 1986, Hughes and Gammon 1987). The percentage of individuals that are alien reflects biological pollution, which has usually been less reversible than chemical and physical disturbance (Hughes et al. 1998); it was the second most commonly cited cause of fish species extinction after physical habitat change (Miller et al. 1988). Likewise, the proportion of tolerant, warmwater adapted individuals tends to increase as a result of habitat degradation and/or water quality degradation of coldwater streams (Lyons et al. 1996, Maret 1997).

Changes in the biotic integrity of streams can be expressed by the trophic composition of the fish assemblage. For example, organic pollution entering streams alters food sources, resulting in changes to the trophic structure of fish assemblages (Karr et al. 1986). These enriched conditions favor tolerant omnivorous individuals that adapt easily to disrupted food sources. The proportion of omnivores (primarily common carp and some catostomid species) increases with human disturbance in western rivers (Hughes and Gammon 1987, Maret 1997).

The proportion of individuals occupying a particular habitat type is useful for evaluating the effects of altered physical habitat (Karr et al. 1986). For example, the number of native "hider" species, which are commonly found in substrate interstices or among macrophytes or organic debris, tends to decline with habitat disturbance (Hughes et al. 1998). The number of small benthic dwelling species (sculpins and dace), large benthic species (suckers), or both have been recommended as indicators of biotic integrity (Karr et al. 1986, Hughes and Gammon 1987). Other benthic species metrics such as number of cottid age classes may provide useful information as well.

Although it is not our intent to develop a multimetric index in this paper, an essential step in the development process is publication of metric classifications for the fish species in this region for widespread review and comment. This type of fish species information previously has been inconsistent and separately located. Our goal is to provide a single information source so scientists can more effectively use fish assemblage information in their assessments of the condition of surface waters. We offer consistent species classifications that are applicable to surveys across the Pacific Northwest, large portions of its states, or at site and watershed scales.

Methods

We compiled a list of freshwater fish species known to occur in Idaho, Oregon, and Washington from species descriptions by Bond (1963, 1973, 1994), Scott and Crossman (1973), Moyle (1976), Wydoski and Whitney (1979), Lee et al. (1980),

Simpson and Wallace (1982), McPhail and Lindsey (1986), Minckley et al. (1986), Sigler and Sigler (1987, 1996), Robins et al. (1991), Behnke (1992), Moseley and Groves (1992), Mongillo (1993), Mongillo and Hallock (1995), and the Washington Department of Natural Resources (1997). A number of estuarine and brackish water species were also listed if commonly found in freshwater fish collections. We used the scientific and common names of species as listed by Robins et al. (1991).

A set of attributes believed responsive to or indicative of human disturbance was selected. Additionally, these attributes were assumed to reflect either biological processes or criteria contained in state water quality standards. We based our species classifications on the accounts from the authors cited in the preceding paragraph, plus Carlander (1969, 1977), National Academy of Sciences and National Academy of Engineering (1972), Minckley (1973), Pflieger (1975), Coutant (1977), Hokanson (1977), Trautman (1981), Becker (1983), Smith (1985), Woodling (1985), Courtenay et al. (1986), Ohio Environmental Protection Agency (1987), Bond et al. (1988), Robison and Buchanan (1988), Page and Burr (1991), Rinne and Minckley (1991), LaRivers (1994), Baxter and Stone (1995), and our aggregate experience. The personal observations of the authors and reviewers were used in instances where sources disagreed on a particular species classification or if no information was available.

Each Pacific Northwest freshwater fish species was classified as either native or alien on a state by state basis. We defined native species as those believed to have been present in the state prior to European settlement. Alien species were those that are introduced through human intervention in a given state or in the region.

We classified the overall pollution tolerance of species as sensitive (S), tolerant (T), or intermediate (I). Sensitive species were those that tend to either disappear or are greatly reduced in association with human disturbances (Karr et al. 1986). These species are typically intolerant of siltation, turbidity, increased water temperature, and lowered dissolved oxygen and tend to be replaced by intermediate and tolerant species. We defined tolerant species as fishes that tend to increase in abundance with human disturbances, particularly in relation to increased siltation, turbidity, and water temperature, and lowered concentrations of dissolved oxygen. Species that tend to be neither tolerant nor sensitive to increased siltation, turbidity, temperature, or lowered dissolved oxygen, but are typically replaced by tolerant species in those situations, were considered intermediate. Species classified as having intermediate tolerance are unlikely to be useful indicators in highly disturbed waters with very poor water quality. However, where the disturbance is limited to moderate degradation of high quality waters or where it is mostly an alteration of physical habitat structure, these species are expected to be useful indicators.

Adult habitat attributes were classified as benthic, water column, or hider to help detect human induced changes to habitat structure (Oberdorff and Hughes 1992, Simon and Lyons 1995, Hughes et al. 1998). Benthic species were those that typically occur on or near the bottom of lakes or streams. Water column species were fish that tend to occur throughout the various depths or near the water surface. Fish species classified as hiders were commonly found buried in sediments or hidden in dense cover such as aquatic macrophytes, undercut banks, crevices, or overhanging vegetation.

Changes in food resources can cause shifts in the trophic structure of fish assemblages (Karr et al. 1986). To detect effects of human disturbances on the aquatic food web, we classified Pacific Northwest fishes into six feeding groups based on literature descriptions of primary diet and distinguishing anatomy. Our classifications of adult feeding attributes also include the freshwater juveniles of anadromous or non-feeding adult species. We defined feeding groups as filterer, herbivore, omnivore, invertivore, piscivore/invertivore, and piscivore. Filterers ingest fine particles from the water column and typically have modified mouth parts or gill rakers for filtering. Herbivores feed primarily on aquatic vegetation, typically have mouth parts modified for scraping, and have an elongated gut to aid in digestion of cell walls. Species classified as omnivores primarily eat plant and animal material (at least 25% of each). Invertivores consume invertebrate prey, primarily insects. Piscivore/invertivores eat considerable proportions of fish and invertebrates and typically have an enlarged mouth relative to non-piscivorous species. Piscivores primarily consume fish and usually have numerous teeth, large eyes, and large mouths.

To assess the effects of human induced changes on the thermal regime of water resources, we classified fish species as cold water, cool water, or warm water (Hokanson 1977, Eaton et al. 1995). We determined the temperature classifications from species ranges, spawning seasons, spawning temperatures, and physiological optima (Hokanson 1977).

Results and Discussion

We provide classifications of origin, overall pollution tolerance, adult habitat, adult feeding, and water temperature for 132 species of freshwater fish known to occur in the Pacific Northwest (Table 1). Of these species, 78 occur in Idaho, 104 in Oregon, 85 in Washington, and 53 species are common to all three states. There are 2, 9, and 1 fish species endemic to the three respective states.

To demonstrate ichthyogeographic patterns in classifications of fish species attributes, we provide state and regional examples (Figure 1). Fifty of the 132 freshwater fish species in the Pacific Northwest are aliens. The numbers of species that are alien to Idaho, Oregon, and Washington are 38, 38, and 36, respectively. Regionally, 37 species are warm-water fish, but 33 of these are aliens. In Idaho, 24 species are classified as warm water (all of these are aliens), while 29 warm water species (26 alien) occur in Oregon, and 20 (19 alien) in Washington. Tolerant species show similar numbers. Regionally, 46 freshwater species are tolerant, 32 of which are aliens. In Idaho, Oregon, and Washington, 30, 37, and 24 of the species are tolerant, respectively. Most of these tolerant species (24, 26, and 18, respectively) are aliens. These comparisons show that, on regional and state scales, the majority of warm water and tolerant fish species are alien and have the potential to significantly disturb fish assemblages in stressed habitats.

To illustrate the use of fish attribute classifications in site evaluations, we examined three markedly different metrics (% alien individuals, % omnivorous individuals, and % sensitive species) from two wadeable and two large river sites in each state (Table 2). Although raw species composition data are useful for fish biologists, it is easier for managers and the public to compare such a set of metric scores. The first site in each pair represents a physically and/or chemically disturbed habitat; these support relatively more aliens, more omnivores, fewer sensitive species, or perhaps all three. The second site in each pair represents less disturbed habitat. These disturbance rankings were made independently of the fish metric percentages. Only reticulate sculpin was collected at the Bone River, Washington site. Since the reticulate sculpin is not classified as alien, omnivorous, or sensitive, it renders these metrics meaningless at this site. Useful metrics may be combined into indices of fish assemblage integrity once reference (minimally impacted or historical) conditions are determined against which metric scores are judged.

To be effective and credible in using fish assemblages to assess the integrity of water resources regionally, biologists must agree on the attribute classifications of the fish species present. These attribute classifications promote interagency and interstate comparisons of fish assemblage integrity at least across our five agencies and three states. For example, since all six large river sites in Table 2 are in similar-sized Columbia River tributaries, their fish assemblages can be compared or ranked by degree of impact from low (Snake River at Flagg), to intermediate (Willamette River at McKenzie, Yakima River at Umtanum), to high (all three disturbed river sites).

Users of these classifications are cautioned that this is a work in progress and at least seven limitations need to be considered.

(1) Much of the information contained in Table 1 was obtained from "fishes of" books as opposed to the primary literature. Such information therefore reflects subjective opinions of the authors as well as our own.

(2) There are substantial biogeographic limitations in applying our classifications. For example, a species that is generally tolerant in the Willamette Valley ecoregion is unlikely to occur in the high elevation Willamette River tributaries of the Coast Range and Cascades. Sites in such places will lack tolerant species as classified here, so intermediate species may be used for assessing disturbance. Similar modifications will apply elsewhere in mountainous regions. Adaptations of local fish stocks or subspecies (e.g. redband trout, Lahonton cutthroat trout) to elevated temperature may require modification of these classifications to increase metric sensitivity. Also, rainbow trout planted in streams inhabited by westslope cutthroat trout must be considered aliens

TABLE 1. Classifications of freshwater fish species known to occur in Idaho, Oregon, or Washington (families listed alphabetically).

Family/Species	Common Name	Origin by State[1]	Overall Tolerance[2]	Adult Freshwater Habitat	Temperature	Adult Freshwater Feeding
Acipenseridae						
Acipenser medirostris	green sturgeon	OR, WA	S	benthic	cold	piscivore
Acipenser transmontanus	white sturgeon	ID, OR, WA	I	benthic	cold	invert/piscivore
Catostomidae						
Catostomus ardens	Utah sucker	ID	T	benthic	cool	omnivore
Catostomus catostomus	longnose sucker	ID, WA	I	benthic	cold	invertivore
Catostomus columbianus	bridgelip sucker	ID, OR, WA	T	benthic	cool	herbivore
Catostomus discobolus	bluehead sucker	ID	I	benthic	cool	herbivore
Catostomus macrocheilus	largescale sucker	ID, OR, WA	T	benthic	cool	omnivore
Catostomus occidentalis	Sacramento sucker	OR	T	benthic	cool	omnivore
Catostomus platyrhynchus	mountain sucker	ID, OR, WA	I	benthic	cool	herbivore
Catostomus rimiculus	Klamath smallscale sucker	OR	I	benthic	cool	omnivore
Catostomus snyderi	Klamath largescale sucker	OR	I	benthic	cool	omnivore
Catostomus tahoensis	Tahoe sucker	OR	I	benthic	cool	omnivore
Catostomus warnerensis	Warner sucker	OR	I	benthic	cool	omnivore
Chasmistes brevirostris	shortnose sucker	OR	S	benthic	cool	invert/planktivore
Deltistes luxatus	Lost River sucker	OR	I	benthic	cool	invertivore
Centrarchidae						
Ambloplites rupestris	rock bass	A	I	water column	warm	invert/piscivore
Archoplites interruptus	Sacramento perch	A	T	water column	warm	invert/piscivore
Lepomis cyanellus	green sunfish	A	T	water column	warm	invert/piscivore
Lepomis gibbosus	pumpkinseed	A	T	water column	cool	invert/piscivore
Lepomis gulosus	warmouth	A	T	water column	warm	invert/piscivore
Lepomis macrochirus	bluegill	A	T	water column	warm	invert/piscivore
Lepomis microlophus	redear sunfish	A	T	water column	warm	invert/piscivore
Micropterus dolomieui	smallmouth bass	A	I	water column	cool	piscivore
Micropterus salmoides	largemouth bass	A	T	water column	warm	piscivore
Pomoxis annularis	white crappie	A	T	water column	warm	invert/piscivore
Pomoxis nigromaculatus	black crappie	A	T	water column	warm	invert/piscivore
Cichlidae						
Cichlasoma nigrofasciatum	convict cichlid	A	T	water column	warm	invert/piscivore
Tilapia aurea	blue tilapia	A	T	water column	warm	invert/piscivore
Tilapia mossambica	Mozambique tilapia	A	T	water column	warm	invert/piscivore
Clupeidae						
Alosa sapidissima	American shad	A	I	water column	cool	invertivore
Cobitidae						
Misgurnus anquillicaudatus	oriental weatherfish	A	T	benthic	warm	omnivore
Cottidae						
Cottus aleuticus	coastrange sculpin	OR, WA	I	benthic	cool	invertivore
Cottus asper	prickly sculpin	OR, WA	I	benthic	cool	invert/piscivore
Cottus bairdi	mottled sculpin	ID, OR, WA	I	benthic	cool	invertivore
Cottus beldingi	Paiute sculpin	ID, OR, WA	I	benthic	cold	invertivore
Cottus cognatus	slimy sculpin	ID, WA	I	benthic	cold	invertivore
Cottus confusus	shorthead sculpin	ID, OR, WA	S	benthic	cold	invertivore

TABLE 1. Classifications of freshwater fish species known to occur in Idaho, Oregon, or Washington (families listed alphabetically).

Family/Species	Common Name	Origin by State[1]	Overall Tolerance[2]	Adult Freshwater Habitat	Temperature	Adult Freshwater Feeding
Cottus extensus	Bear Lake sculpin	ID	I	benthic	cold	invertivore
Cottus greenei	Shoshone sculpin	ID	S	benthic	cold	invertivore
Cottus gulosus	riffle sculpin	OR, WA	I	benthic	cool	invertivore
Cottus klamathensis	marbled sculpin	OR	I	benthic	cool	invertivore
Cottus leiopomus	Wood River sculpin	ID	S	benthic	cold	invertivore
Cottus marginatus	margined sculpin	OR, WA	I	benthic	cool	invertivore
Cottus perplexus	reticulate sculpin	OR, WA	I	benthic	cool	invertivore
Cottus pitensis	pit sculpin	OR	T	benthic	cool	invertivore
Cottus princeps	Klamath Lake sculpin	OR	I	benthic	cold	invertivore
Cottus rhotheus	torrent sculpin	ID, OR, WA	I	benthic	cold	invert/piscivore
Cottus tenuis	slender sculpin	OR	I	benthic	cool	invertivore
Leptocottus armatus	Pacific staghorn sculpin	OR, WA	I	benthic	cold	invertivore
Cyprinidae						
Acrocheilus alutaceus	chiselmouth	ID, OR, WA	I	benthic	cool	herbivore
Carassius auratus	goldfish	A	T	benthic	warm	omnivore
Couesius plumbeus	lake chub	ID, WA	I	water column	cold	invertivore
Ctenopharyngodon idella	grass carp	A	T	water column	warm	herbivore
Cyprinus carpio	common carp	A	T	benthic	warm	omnivore
Gila alvordensis	Alvord chub	OR	T	water column	warm	omnivore
Gila atraria	Utah chub	ID	T	water column	cool	omnivore
Gila bicolor	tui chub	ID, OR, WA	T	water column	cool	omnivore
Gila boraxobius	Borax Lake chub	OR	I	water column	warm	invertivore
Gila coerulea	blue chub	OR	T	water column	cool	omnivore
Gila copei	leatherside chub	ID	I	water column	cool	invertivore
Hesperoleucus symmetricus	California roach	OR	T	benthic	warm	omnivore
Mylocheilus caurinus	peamouth	ID, OR, WA	I	water column	cool	invertivore
Notemigonus chrysoleucas	golden shiner	A	T	water column	warm	omnivore
Oregonichthys crameri	Oregon chub	OR	I	hider	cool	invertivore
Oregonichthys kalawatseti	Umpqua chub	OR	I	hider	cool	invertivore
Pimephales promelas	fathead minnow	A	T	water column	warm	omnivore
Ptychocheilus oregonensis	northern squawfish[3]	ID, OR, WA	T	water column	cool	invert/piscivore
Ptychocheilus umpquae	Umpqua squawfish[4]	OR	T	water column	cool	invert/piscivore
Rhinichthys cataractae	longnose dace	ID, OR, WA	I	benthic	cool	invertivore
Rhinichthys evermanni	Umpqua dace	OR	I	benthic	cool	invertivore
Rhinichthys falcatus	leopard dace	ID, OR, WA	I	benthic	cool	invertivore
Rhinichthys osculus	speckled dace	ID, OR, WA	I	benthic	cool	invertivore
Richardsonius balteatus	redside shiner	ID, OR, WA	I	water column	cool	invertivore
Richardsonius egregius	Lahontan redside	OR	I	water column	cool	invertivore
Tinca tinca	tench	A	I	water column	warm	invertivore
Cyprinodontidae						
Fundulus diaphanus	banded killifish	A	T	water column	warm	invertivore
Lucania parva	rainwater killifish	A	T	water column	warm	invertivore
Embiotocidae						
Cymatogaster aggregata	shiner perch	OR, WA	S	benthic	cold	invertivore
Esocidae						
Esox americanus	grass pickerel	A	I	water column	cool	piscivore
Esox lucius	northern pike	A	I	water column	cool	piscivore

TABLE 1. Classifications of freshwater fish species known to occur in Idaho, Oregon, or Washington (families listed alphabetically).

Family/Species	Common Name	Origin by State[1]	Overall Tolerance[2]	Adult Freshwater Habitat	Temperature	Adult Freshwater Feeding
Gadidae						
Lota lota	burbot	ID, OR, WA	I	benthic	cold	piscivore
Gasterosteidae						
Gasterosteus aculeatus	threespine stickleback	OR, WA	T	hider	cool	invertivore
Ictaluridae						
Ameiurus catus	white catfish	A	T	benthic	warm	invert/piscivore
Ameiurus melas	black bullhead	A	T	hider	warm	invert/piscivore
Ameiurus natalis	yellow bullhead	A	T	hider	warm	invert/piscivore
Ameiurus nebulosus	brown bullhead	A	T	hider	warm	invert/piscivore
Ictalurus furcatus	blue catfish	A	T	benthic	warm	invert/piscivore
Ictalurus punctatus	channel catfish	A	T	benthic	warm	invert/piscivore
Noturus gyrinus	tadpole madtom	A	T	hider	warm	invert/piscivore
Pylodictis olivaris	flathead catfish	A	T	benthic	warm	piscivore
Osmeridae						
Hypomesus pretiosus	surf smelt	OR, WA	S	water column	cold	invertivore
Spirinchus thaleichthys	longfin smelt	OR, WA	I	water column	cool	invertivore
Thaleichthys pacificus	eulachon	OR, WA	I	water column	cool	invertivore
Percichthyidae						
Morone chrysops	white bass	A	I	water column	cool	piscivore
Morone saxatilis	striped bass	A	I	water column	cool	piscivore
Percidae						
Perca flavescens	yellow perch	A	I	water column	cool	invert/piscivore
Stizostedion vitreum	walleye	A	I	water column	cool	piscivore
Percopsidae						
Percopsis transmontana	sand roller	ID, OR, WA	I	hider	cool	invertivore
Petromyzontidae						
Lampetra ayresi	river lamprey	OR, WA	I	hider	cool	filter feeder[5]
Lampetra lethophaga	Pit-Klamath brook lamprey	OR	I	hider	cool	filter feeder[5]
Lampetra minima	Miller Lake lamprey	OR	I	hider	cool	piscivore[5]
Lampetra richardsoni	western brook lamprey	OR, WA	I	hider	cool	filter feeder[5]
Lampetra similis	Klamath River lamprey	OR	I	hider	cool	filter feeder[5]
Lampetra tridentata	Pacific lamprey	ID, OR, WA	I	hider	cool	filter feeder[5]
Pleuronectidae						
Platichthys stellatus	starry flounder	OR, WA	S	benthic	cold	invertivore
Poeciliidae						
Gambusia affinis	western mosquitofish	A	T	water column	warm	invertivore
Poecilia mexicana	shortfin molly	A	T	water column	warm	omnivore
Poecilia reticulata	guppy	A	T	water column	warm	omnivore
Xiphophorus helleri	green swordtail	A	T	water column	warm	omnivore

TABLE 1. Classifications of freshwater fish species known to occur in Idaho, Oregon, or Washington (families listed alphabetically).

Family/Species	Common Name	Origin by State[1]	Overall Tolerance[2]	Adult Freshwater Habitat	Temperature	Adult Freshwater Feeding
Salmonidae						
Coregonus clupeaformis	lake whitefish	A	I	water column	cold	invertivore
Oncorhynchus aguabonita	golden trout	A	S	hider	cold	invert/piscivore[5]
Oncorhynchus clarki	cutthroat trout	ID, OR, WA	S	water column	cold	invert/piscivore
Oncorhynchus gorbuscha	pink salmon	OR, WA	S	water column	cold	invertivore[5]
Oncorhynchus keta	chum salmon	OR, WA	S	water column	cold	invertivore[5]
Oncorhynchus kisutch	coho salmon	ID, OR, WA	S	water column	cold	invertivore[5]
Oncorhynchus mykiss	rainbow trout	ID, OR, WA	S	hider	cold	invert/piscivore
Oncorhynchus nerka	sockeye salmon	ID, OR, WA	S	water column	cold	invertivore[5]
Oncorhynchus tshawytscha	chinook salmon	ID, OR, WA	S	water column	cold	invertivore[5]
Prosopium abyssicola	Bear Lake whitefish	ID	I	water column	cold	invertivore
Prosopium coulteri	pygmy whitefish	ID, WA	I	water column	cold	invertivore
Prosopium gemmiferum	Bonneville cisco	ID	S	water column	cold	invertivore
Prosopium spilonotus	Bonneville whitefish	ID	I	water column	cold	invertivore
Prosopium williamsoni	mountain whitefish	ID, OR, WA	I	benthic	cold	invertivore
Salmo salar	Atlantic salmon	A	S	water column	cold	invert/piscivore[5]
Salmo trutta	brown trout	A	I	hider	cold	invert/piscivore
Salvelinus alpinus	Arctic char	A	S	hider	cold	invert/piscivore
Salvelinus confluentus	bull trout	ID, OR, WA	S	hider	cold	invert/piscivore
Salvelinus fontinalis	brook trout	A	I	hider	cold	invert/piscivore
Salvelinus malma	Dolly Varden	WA	S	hider	cold	invert/piscivore
Salvelinus namaycush	lake trout	A	S	benthic	cold	piscivore
Thymallus arcticus	Arctic grayling	A	S	water column	cold	invert/piscivore
Umbridae						
Novumbra hubbsi	Olympic mudminnow	WA	T	hider	warm	invertivore

[1] A = alien (non-native, exotic, or introduced) to all three states. ID = native to Idaho, OR = native to Oregon, WA = native to Washington (Does not imply occurrence in all three states.)
[2] I = intermediate species, S = sensitive species, T = tolerant species
[3] recommended for name change to northern pikeminnow (Nelson et al. 1998)
[4] recommended for name change to Umpqua pikeminnow (Nelson et al. 1998)
[5] characterizes most of freshwater life

even though they are native to the state. In other words, regional classifications may require modification when applied at local scales.

(3) A key consideration in developing metrics or biotic indices is that they should detect a range of conditions for the various water bodies assessed. If metrics or indices fail to detect a range of conditions, it may be a result of nondiscriminating species classifications given the fish fauna present. Before developing an index, the fish species present and their classifications must be examined to ensure that a sufficient range of characteristics occurs in the classifications of interest. If there are only sensitive native species present in headwater mountain streams, the overall tolerance and origin classifications cannot be responsive to disturbance, so substitute metrics will be needed.

(4) Although all life stages should be considered in making assessments about fish assemblage integrity (Angermeier and Karr 1986, Northcote 1997), the number of young-of-year individuals is largely stochastic (Yant et al. 1984) and such variability adds an undesirable amount of error into metric interpretation. In addition, survival of young-of-year fishes into later age classes is a better indicator than mere presence or even abundance

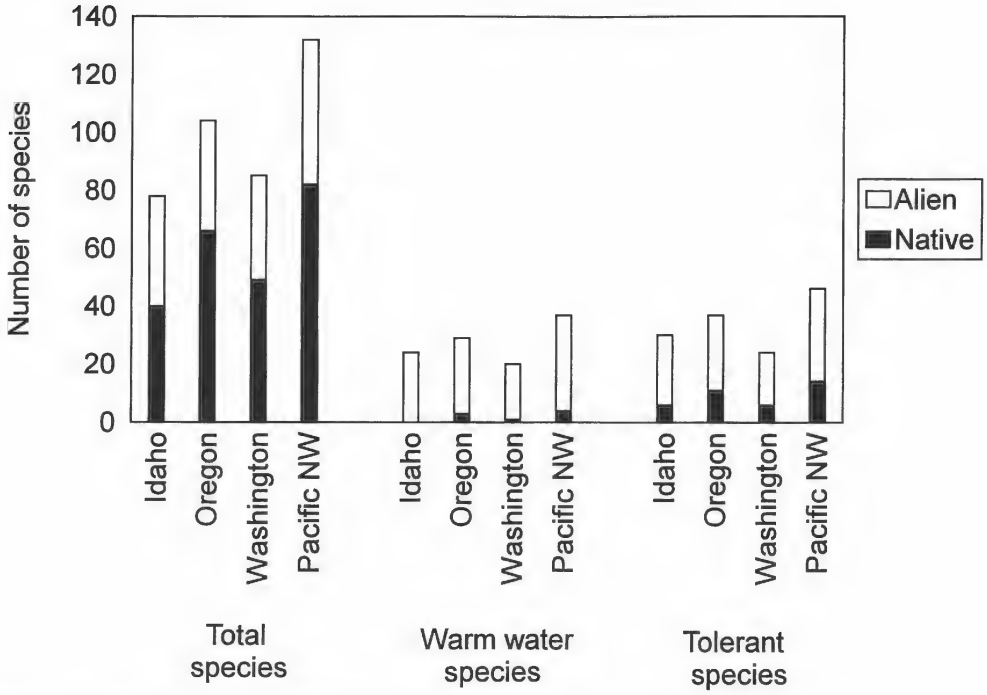

Figure 1. State and regional patterns in origin, temperature, and tolerance attributes.

of young-of-year (Karr et al. 1986), especially in species rich waters. However, where only one to three species of fish exist, as is common in many Pacific Northwest mountain streams, it is essential to collect and assess all life stages, simply to determine if the site can support them all. The emphasis in such cases should be on the presence of the life stages rather than attempting accurate counts of all individuals.

(5) Sampling effort must be sufficient to obtain nearly all species present in a reach at their relative abundances, and fish collected must be identified to the species level. This is especially critical for sculpins, a family that is often identified only to genus. Examination of Table 1 indicates marked differences in overall tolerance and temperature preference among cottid species, which is lost without accurate identification. Fish ecologists should learn to identify all the fish species in their study areas or collect specimens for identification by experts.

(6) Specimen vouchering is critical as a quality assurance and control measure. Museum specimens are crucial for advancing our knowledge of taxonomy and distribution. They also offer the most irrefutable evidence of a collection. To be most useful, specimens must be properly preserved (kill in 10% formalin, slit specimens greater than 15 cm long, and provide ample space in jars to allow for thorough tissue fixing). If specimens are allowed to die and are preserved later, they produce poor quality specimens. This is especially true if the holding water and air temperatures are warm. Collection sites must also be accurately located, preferably by latitude and longitude, using a geographic positioning device so the data can be easily manipulated in a geographic information system.

(7) Additional research on water temperature and feeding preferences of fish species and more thorough distributional studies of fishes would improve our attribute classifications. We found

TABLE 2. Example of metric scores for the proportion of alien species, omnivorous species, and sensitive species from paired wadeable (w) streams and large river (l) sites that represent disturbed and less disturbed physical or chemical habitats in Idaho, Oregon, and Washington.

Site and (type)	Condition	% Alien Individuals	% Omnivorous Individuals	% Sensitive Species
Idaho				
Malad River (w)[1]	disturbed	60	47	0
Little Wood River (w)[2]	less disturbed	3	0	40
Snake River @ Buhl (l)[3]	disturbed	16	45	0
Snake River @ Flagg (l)[4]	less disturbed	5	1	25
Oregon				
Spoon Creek (w)[5]	disturbed	100	0	0
Smallman Creek(w)[6]	less disturbed	0	0	14
Willamette River @ Portland (l)[7]	disturbed	19	27	0
Willamette River @ McKenzie (l)[8]	less disturbed	0	45	23
Washington				
Bone River (w)[9]	disturbed	0	0	0
Mill Creek (w)[10]	less disturbed	0	0	66
Yakima River @ Kiona (l)[11]	disturbed	17	46	0
Yakima River @ Umtanum (l)[12]	less disturbed	0	32	14

[1] black bullhead, common carp, largescale sucker, redside shiner, smallmouth bass (Maret 1997).

[2] brook trout, mountain whitefish, rainbow trout, speckled dace, Wood River sculpin (Maret 1997).

[3] chiselmouth, common carp, largescale sucker, mottled sculpin, northern squawfish, peamouth, rainbow trout, redside shiner, speckled dace, Utah chub (Maret 1997).

[4] brook trout, brown trout, cutthroat trout, longnose dace, mottled sculpin, mountain sucker, mountain whitefish, Paiute sculpin, rainbow trout, redside shiner, speckled dace, Utah sucker (Maret 1997).

[5] largemouth bass, warmouth, western mosquitofish, white crappie, yellow bullhead (Hughes et al. 1998).

[6] brown bullhead, cutthroat trout, redside shiner, reticulate sculpin, speckled dace, threespine stickleback, western brook lamprey (Hughes et al. 1998).

[7] common carp, largemouth bass, largescale sucker, northern squawfish, prickly sculpin, reticulate sculpin, yellow perch (Hughes and Gammon 1987).

[8] chinook salmon, chiselmouth, largescale sucker, mountain sucker, mountain whitefish, northern squawfish, Paiute sculpin, peamouth, rainbow trout, redside shiner, reticulate sculpin, speckled dace, torrent sculpin (Hughes and Gammon 1987).

[9] reticulate sculpin (Merritt et al. 1999).

[10] coho salmon, cutthroat trout, riffle sculpin, speckled dace, torrent sculpin, western brook lamprey (Merritt et al. 1999).

[11] bridgelip sucker, largescale sucker, mountain whitefish, northern squawfish (Cuffney et al. 1997).

[12] bridgelip sucker, chiselmouth, largescale sucker, mountain sucker, mountain whitefish, northern squawfish, rainbow trout (Cuffney et al. 1997).

few comprehensive regional studies documenting the diets of fishes of the Pacific Northwest and the temperatures at which they are most successful. When and where sufficiently large databases allow them, data analyses are needed along gradients of habitat and human disturbance. Finally, better information concerning reproduction and longevity might lead to additional attribute classifications.

In summary, we produced attribute classifications for the freshwater fishes of the Pacific Northwest and demonstrated their applicability in evaluating 12 sites. Additionally, attribute classifications were used to compare species richness, origin, overall pollution tolerance, and water temperature preference in Idaho, Oregon, and Washington. We recognize that our classifications will change with further research and local applications. We

encourage additional study of life histories, autecology, and distributional patterns of non-salmonid Pacific Northwest freshwater fishes. We hope this attribute classification will stimulate more fish ecologists to assess entire fish assemblages, either by direct application of these metrics or by incorporating them in fish assemblage indices. We also want this paper to stimulate criticism and improvement of these classifications and encourage communications by readers to further that end.

Acknowledgements

Motivational support was provided by the Pacific Northwest Bioassessment Work Group and Gretchen Hayslip, USEPA Region 10. M. Hallock provided comments regarding species distributions in Washington. Helpful comments on manuscript drafts were provided by C. Bond, S. Brenkman, W. Clark, G. Larson, H. Li, D. Markle, P. Mongillo, B. Rieman, E. Schreiner, T. Short, and R. Wallace. We also thank the many American Fisheries Society professionals that supplied comments and information on species attributes. The support of the Orma J. Smith Museum of Natural History and Albertson College of Idaho is greatly appreciated. This paper was supported by the Environmental Monitoring and Assessment Program (EMAP), partially funded through contract 68-C6-0005 to Dynamac, and subjected to Environmental Protection Agency peer and administrative review and approved for publication.

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Received 6 October 1998
Accepted 5 April 1999

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Habitat Relations of *Corydalis aquae-gelidae*, a Rare Riparian Plant

Abstract

The relationships between the environment and the abundance of *Corydalis aquae-gelidae*, an herbaceous perennial and a USFWS species of concern, were explored. Information concerning habitat relations was pursued to determine possible conservation measures. *Corydalis* grows in headwater streams, up to 1300 m elevation, and down to 585 m on the fifth order Clackamas River, Mt. Hood National Forest, Oregon. Occupied streams had smaller seasonal flow fluctuations than streams where the species was absent, and had summer air and substrate temperatures averaging 17.7 C and 10.6 C, respectively. *Corydalis* abundance in plots was related to the distance to the summer water level, substrate texture and organic matter content, and plant community composition. Optimal conditions were identified: coarse, moss-covered, mineral substrates within 15 cm of the summer water level. Fine (<2 mm) or organic substrate material reduced *Corydalis* abundance. On the Oak Grove Fork, about 75% of the plants grew between the average winter high and summer low water level, an estimated vertical distance of 25 cm. The results were useful for management, and underscored the need to maintain stable hydrological conditions, avoid sedimentation, and protect riparian areas.

Introduction

Maintaining plant diversity has become a major objective of land management in the Pacific Northwest (USDA-FS, USDI-BLM 1994). Central to this effort is maintaining or enhancing the populations of rare species. One major cause of rarity is that a species may require a habitat that is itself rare (Rabinowitz 1981). Thus, management of habitat should be required to maintain species diversity, and information about habitat requirements of rare species may be necessary for effective management.

Corydalis aquae-gelidae Peck and Wilson (Fumariaceae, cold-water corydalis) has a limited range on the west slopes of the Cascade Range, both north and south of the Columbia River. It is considered a species of concern by the US Fish and Wildlife Service, and is a candidate for listing under the Oregon Endangered Species Act (Oregon Natural Heritage Program 1995). As an uncommon old-growth associated species, it is protected under the Northwest Forest Plan (USDA-FS, USDI-BLM 1994). *Corydalis aquae-gelidae* is restricted to streamside habitats, but details of its habitat requirements are not well known. Streamside plants may be particularly sensitive to impacts from management, because they are affected both by changes in the stream, as well as those in adjacent riparian and hillslope lands. Because upstream roads and clear-cuts can increase peak flows (Jones and Grant 1996), distant, downstream populations could be affected. *C. aquae-gelidae* population size and plant development were previously studied (Goldenberg 1992, Goldenberg and Zobel 1997). In this study, the environmental factors in natural populations within much of the species' range are described, including hydrologic regime, temperature, substrate, and associated vegetation. Based on these habitat characteristics, recommendations for management of the species were developed.

Study species

Corydalis aquae-gelidae is a large perennial herb. Its annual stems arise from large, fleshy taproots and grow to over one meter tall. The species does not spread rhizomatously, unlike the sympatric *C. scouleri*. *C. aquae-gelidae* has high habitat specificity, and is narrowly endemic (Goldenberg 1992). It grows within the *Tsuga heterophylla* and *Abies amabilis* forest zones of Franklin and Dyrness (1973), in Clackamas and Multnomah Counties, Oregon, and Clark and Skamania Counties, Washington (USDA Forest Service 1983, Oregon Natural Heritage Program 1990). An outlying population grows west of Mount St. Helens, in Cowlitz County, Washington. The lowest elevation site is at 460 m, near Tanner Creek in the Columbia River Gorge, while the upper elevational limit is at 1300 m, near Squaw

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Mountain. Within the Mt. Hood National Forest, the total number of reproductive adult *C. aquae-gelidae* plants was estimated at 8,400 (Goldenberg 1992). The total number of reproductive adults throughout the range of the species is 10,000 to 15,000. Its streamside habitat has been subject to disturbance by logging, fish habitat manipulation, and water diversion for hydropower (Goldenberg 1992). Detailed habitat data are needed to facilitate conservation of this species.

Methods

Data were collected 29 June to 8 September 1990, and 9 July to 10 September 1991. Study sites included known populations in the southwestern portion of the Mount Hood National Forest, Oregon (44° 55' to 45° 15' N latitude and 121° 50' to 122° 15' W longitude); this area supports most plants of the species (USDA Forest Service 1983, Oregon Natural Heritage Program 1990). Plots were located on and near two larger river reaches, the upper Clackamas River near Big Bottom, and the Oak Grove Fork of the Clackamas River; these plots occurred at 600 to 1006 m elevation. Plots were also located on small streams and springs to the northwest of these rivers, near Soosap Peak and near Squaw Mountain. These headwater populations occurred at 840-1250 m. Most of the sites were bordered by late-successional forest, except for eight plots from two sites in the Soosap Peak area, which had been clearcut in 1971.

In 1990, each of 75 1-m^2 plots was centered on an adult plant randomly selected from each 200 encountered during a population census. During 1991, for each of 25 plots centered around a selected adult, two additional plots were sampled, one upstream and one downstream. These additional plots were located at a random distance between 5 and 15 meters from the sample plant, and between 2 meters into and 3 meters away from the stream edge. Eleven of the additional plots included *Corydalis*. The 39 plots without *Corydalis* were used to compare nearby microsites that lacked the species. There were 150 plots in total.

To determine the abundance of *Corydalis aquae-gelidae,* we recorded percent cover, numbers of individuals in each of four growth stages, and average height and leaf numbers of the largest three adults. The four growth stages were seedlings (first year plants with cotyledons, almost never with a true, compound leaf), juveniles (plants with one or more true, compound leaves, but no cotyledons or above-ground stems), nonreproductive adults (plants with one or more aboveground stems), and reproductive adults. These growth stages corresponded to obvious morphological breaks among different sizes of plants.

For each 1-m^2 plot, we recorded air, substrate and water temperature; horizontal distance to water; vertical distance to water; water cover percent; surface cover percent of moss, mineral and organic material; surface cover percent of stones (>250 mm), cobbles (76 to 250 mm), gravel (2 to 76 mm), and fines (<2 mm, sand, silt, clay, and highly decomposed organic material); substrate type, including gravel and coarse sand (GS), gravel and sand dominant, with additional soil, mud or organic material (GX), and soil or mud dominant (LX); canopy cover percent; canopy species (shrubs and trees over 1 m above the plot); and understory species (species with cover below 1 m). Taxonomic nomenclature followed Hitchcock and Cronquist (1973). Air temperature was recorded in the sample plant's canopy, while substrate and water temperature was recorded at about 10 cm depth; these data were recorded at the time the plots were sampled. In forty plots occupied by *Corydalis aquae-gelidae*, a soil sample of about 1 L was sifted through a 2 mm sieve. Gravel, coarse (>2mm) organic material, and fine material were measured volumetrically.

Statistical Analyses

The seven variables indicating *Corydalis aquae-gelidae* abundance were transformed (natural logarithm or square root) to approximate bivariate normality on all pairwise comparisons (scatterplots were used to assess the relationship), and standardized as (X_i - mean)/standard deviation. Principal components analysis (using Statgraphics, STSC 1991) was used to combine abundance variables into two indices of abundance: a reproduction index (combining seedling and juvenile numbers) and a biomass index (combining cover, adult numbers multiplied by average leaf number, and adult numbers times average height). A constant was added to the indices to increase their minima to zero, corresponding to zero for the original variables. The dry mass of *Corydalis* plants was correlated with both their height and leaf numbers (r^2=0.96, 0.98, respectively, Goldenberg 1992); hence height and leaf num-

bers multiplied by the adult density correlated with the biomass in the plot. In addition, leaf number was correlated with pedicel numbers (r^2=0.87), and therefore with seed production.

Plant community ordination scores were calculated for each 1-m^2 plot, separately for canopy and understory species (exclusive of *Corydalis aquae-gelidae*) using PC-Ord (McCune 1991). Because of the wide variety of sites sampled and the small plots, the species by sample data matrices were largely zeroes (94% for the understory, 89% for the canopy). Therefore, the data matrices were transformed using the sociological favorability index (Beals 1984), which uses binary data. Bray-Curtis ordination (using city-block distance and variance-regression endpoint selection, Beals 1984) then extracted 48% of the understory variation on the first three axes. Ordination on the canopy species extracted 77% of the variation on the first three axes. A non-metric multidimensional scaling ordination analysis (NMS, Kruskal 1964) was run on the Bray-Curtis ordination scores. For the understory, both Bray-Curtis and NMS results are reported here. The results from NMS were used for the canopy species.

A smoothing procedure was used to relate environmental variables to *Corydalis aquae-gelidae* abundance indices. Reproduction and biomass index scores were ordered based on the scores for each of the environmental variables. The resulting ordered series (of reproduction or biomass index) were put through a smoothing procedure. Running averages were calculated using values from varying "windows" within the range of dependent variable data, with the average y value calculated where the x value is within +/- a chosen percent of the x range. For example, if the independent (x axis) variable ranged from 1 to 100, and a 10% window was chosen, all y values corresponding to x values between 40 and 60 were used to calculate the average y value at x = 50. Different windows were used to find an appropriate smoothed line, i.e., a line that removes excess scatter without becoming excessively flat. A visual basic algorithm was written in Excel (Microsoft 1993) to calculate the averages. This procedure produced a better fit to the data than a standard running average. This variation on the classic moving average is similar to LOWESS smoothing (Cleveland 1981), in that an average of y values is calculated based on the associated x values.

Spearman's rank correlation was used to test for statistical significance. Coefficients were calculated separately above and below optima, which were located by inspection of graphs generated using the smoothing procedure.

Time dependency was tested graphically and by linear regression; sample date or time of day was not correlated with the other variables, except as mentioned below.

The above statistical methods, smoothing and rank correlation, were chosen over parametric regression techniques because of the variability and complexity of the relationships. Also, regression could not be applied without violating the assumptions. The non-parametric methods chosen have few assumptions or limitations. Some measure of subjectivity is inherent in smoothing procedures, however, as the level of smoothing is chosen by the researcher. The rank correlations are limited to monotonic relationships, hence the separate analyses on different sides of the graphically chosen optima.

Results

Corydalis aquae-gelidae Abundance Indices

The two indices calculated to represent the biomass and reproductive success of *Corydalis aquae-gelidae* accounted for most of the variance in the input variables: the reproduction index (first PCA axis), 86%, and the biomass index, 96%. The two indices were correlated (r^2=0.48, P<0.0001) but graphing showed that reproduction was not necessarily high where adult biomass was high. The average values of the original variables that corresponded to given index values were calculated (Table 1). There was a gap in the values for the biomass index, due to few samples with small adults.

Geomorphology

Corydalis aquae-gelidae grew in a narrow band (in the active channel of Gregory et al. 1991) along streams of many sizes. Occupied headwater streams (smaller than first order) were mainly at high elevations in the Squaw Mountain and Soosap Peak areas. The largest stream was the fifth order channel of the upper Clackamas River, with *Corydalis* occurring down to 585 m elevation. Where *Corydalis* was present, adult abundance

TABLE 1. Correspondence of original *Corydalis aquae-gelidae* abundance variables with abundance indices. The equations defining these indices were:

1) Reproduction index = 0.71 ln(seedlings, no./m^2 + 1) + 0.71 ln(juveniles, no./m^2 + 1)
2) Biomass index = 0.57 (cover %)$^{1/2}$ + 0.58 ln(height, cm * adults, no./m^2 + 1) + 0.58 ln(no. of leaves * adults, no./m^2 + 1)

Index	Variable	Value of the index					
		0	1	2	3	4	5
Reproduction	Seedling numbers	0	1.6	5.5	15.6	41	*
	Juvenile numbers	0	1.9	7.5	23.8	71	*
Biomass	Adult numbers	0	0	1	2	4	13
	Leaf numbers	0	0	2	7	40	330
	Height (cm)	0	5	20	46	82	128
	Cover%	0	4	15	34	60	94

* The reproduction index does not exceed 4.

(the biomass index) varied significantly among stream orders (ANOVA, P=0.03), but the reproduction index did not. The largest, densest plants (high biomass index) grew along the largest streams. *Corydalis* abundance indices did not vary significantly with sample plot elevation.

River Flow Fluctuations

Streams occupied by *Corydalis aquae-gelidae* exhibited little bare gravel and rock above the summer water level, less than many streams without the species. Streams supporting the species apparently had less seasonal flow fluctuation. Gaging station data from the southwest Mount Hood National Forest supported this hypothesis. The coefficient of variability for annual and growing season stream flow fluctuation (standard deviation/mean of mean monthly flows) was lower for occupied stream reaches (0.24 to 0.35) than for unoccupied streams (0.40 to 0.73, P=0.01, n=8, one-tailed rank sum tests). The average annual stream flow (i.e., stream size) did not differ significantly between reaches occupied by *Corydalis* and other reaches, nor did the difference between high and low flow in cubic meters per second.

The relationship of *Corydalis aquae-gelidae* to seasonal river levels was explored. River flow data (Bingham Engineering 1985) for the Oak Grove Fork below Stone Creek were transformed into river surface levels using the relationship for the gaging station. This relationship varies downstream, depending on the bed shape. These distances were relativized to the mean July water level. Data points for each month in Figure 1 include the mean of monthly means for 25 years, and 25-year maximum and minimum monthly means. The growing season is generally late May through early September. This reach of the Oak Grove Fork is downstream from a dam, which regulates the stream flow.

During July, 1990, on the Oak Grove Fork, the lowest plant was rooted at 14 cm below the water surface, the median was 7 cm above (n=97), 95% of the plants were within a vertical range of 25 cm, and the highest plant was at 95 cm above the water surface. Measured plant locations were used to estimate the number of *Corydalis* plants that would be submerged (at least partially) under the river levels in Figure 1, yielding Figure 2, which shows that about 75% of the plants occupy the zone between average summer low and winter high water level.

Microsite Temperature Patterns

Corydalis aquae-gelidae grew in a cool environment. During field sampling, water temperature averaged 9.7°C (SD 2.0, range 5.2 to 14.1), substrate temperature averaged 10.6°C (SD 2.3, range 5.4 to 18.9), and air temperature averaged 17.7°C (SD 3.8, range 8.9 to 29.8). Because the substrate was often submerged, many plots had a similar water and substrate temperature. A regression model was built for temporal changes in air temperature:

Air temp. (°C) = -20.8 - 0.025(date) + 5.4(time) - 0.18(time^2)
R^2=0.15 P<0.0001 n=150

Date was calculated as days since June 21. Time is in hours; minutes were transformed to decimals

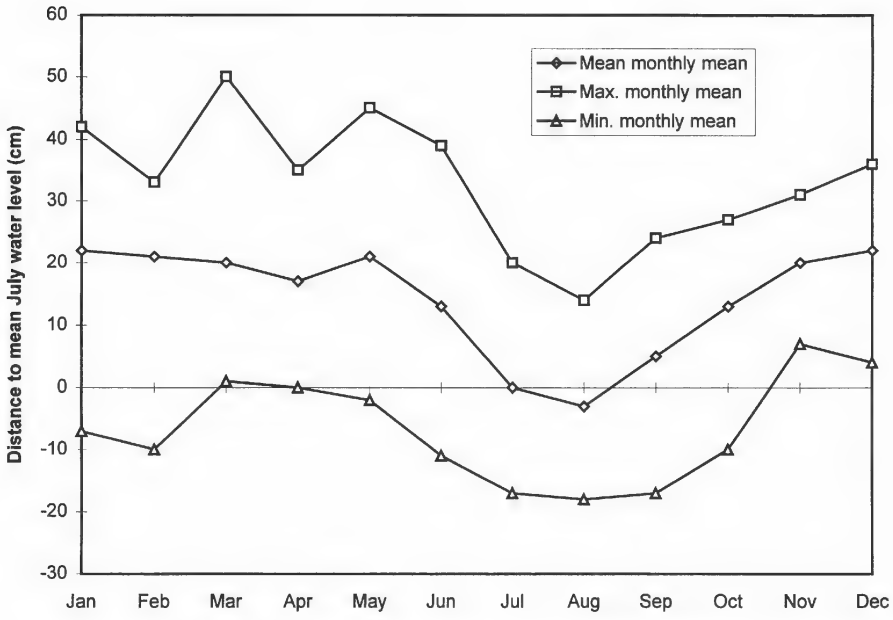

Figure 1. Average river level on the Oak Grove Fork as vertical distance to mean July water level. For 25 years on record.

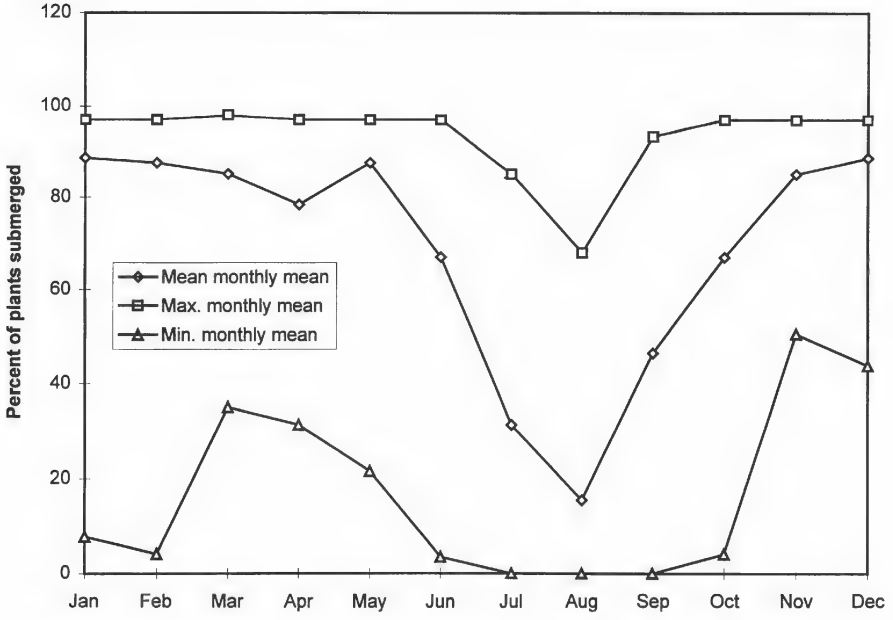

Figure 2. Average percent of adult *Corydalis* plants at least partially submerged.

of hours. The predicted July average maximum air temperature was 19.1 °C, cooler than July maxima for weather stations in these forest zones, which are 21 to 27 °C.

Substrate Analyses

Three types of substrates occurred in the sample plots. Gravel and sand (GS) substrates were stream sediments. Substrates containing gravel, sand and other materials (GX type substrates) represented mostly streambed deposits with additional siltation or organic matter deposition. Various loams or mud substrates (LX types) represented forest soils with litter layers, or deposits within the stream bed, often in marsh or swamp areas. Substrate components differed among the substrate types (Table 2).

Community Composition Ordinations

The positions of sample plots on axes produced by the understory and canopy community ordinations were correlated with environmental variables, especially elevation (Spearman rank correlation, r_s, .51 to .53), stream order (r_s .57 to .66), proximity to water (r_s .21 to .29), and substrate composition (r_s .01 to .36). The Bray-Curtis method gave results similar to the NMS ordination method. High values on the first understory axis indicated species of the wettest habitats (e.g., *Glyceria elata*, *Veronica americana*, *Oenanthe sarmentosa*, *Stachys cooleyae*, and *Petasites frigidus*), particularly on the larger, low elevation streams. Low understory axis values indicated species of either wet habitats with fine substrates or moist forest habitats (e.g., *Blechnum spicant*, *Trautvetteria caroliniensis*, *Cornus canadensis*, and *Tiarella trifoliata*); these latter species were often of higher elevations. The most frequent understory species were *Epilobium glandulosum* and *Mimulus guttatus*, which indicated intermediate axis values. Other species that had intermediate understory axis values include *Circaea alpina, Galium triflorum, Mitella ovalis, Montia sibirica,* and *Tolmiea menziesii*. For the canopy axis, high values indicated dense *Tsuga heterophylla* and high elevation canopy species (e.g., *Abies amabilis*, *Alnus sinuata*); low values indicated less dense canopies found on the larger rivers (e.g., *Thuja plicata*, *Alnus rubra*).

Response to Microsite Variables

The abundance indices differed significantly among the substrate types (Table 3). 34 of 64 correlations between the environmental variables and *Corydalis aquae-gelidae* abundance indices were statistically significant at alpha =0.05 (Table 4, 5). *Corydalis aquae-gelidae* abundance was related

TABLE 3. Median values of the reproduction and biomass indices for the three types of substrates (described in Table 2).

A. For all Plots. Significantly different among the substrate types (P=0.0002, reproduction index, P<0.0001, biomass index, Kruskal-Wallis test).

Type	n	Median Reproduction Index	Median Biomass Index
GS	73	1.64	3.53
GX	40	1.04	3.11
LX	36	0.0	0.0

B. For plots within the optimal range of water levels. Significantly different among the substrate types (P=0.006, reproduction index, P=0.0001, biomass index, Kruskal-Wallis test).

Type	n	Median Reproduction Index	Median Biomass Index
GS	54	2.06	3.63
GX	34	1.11	3.23
LX	16	0.29	0.09

TABLE 2. Substrate components (%) by substrate type. Components were measured volumetrically in 40 samples, within plots with *Corydalis aquae-gelidae*. GS substrates consisted of only gravel and sand. GX substrates are mostly gravel and sand, with other materials prevalent. LX substrates are mostly soil or mud, with other materials additionally. Fines are all materials less than 2 mm, including sand, silt, clay and organic matter. Standard deviations in parentheses.

Type	n	Gravel	Sand	All fines	Organic (>2mm)
GS	17	75 (12)	25 (12)	NA	NA
GX	17	57 (12)	NA	32 (17)	11 (10)
LX	6	19 (21)	NA	72 (19)	8 (7)

TABLE 4. The abundance of *Corydalis aquae-gelidae* correlated to environmental variables: results for the reproduction index. r and P values refer to Spearman rank correlations. Bray-Curtis (BC) and NMS are alternative ordination methods. Variables with significant correlations (alpha=0.05) are reported. Optima were determined by inspection of scatterplots. Generally, abundance increases to the optima (positive r), and decreases after the optima (negative r).

Variable	Optimum	<Optimum			>Optimum		
		n	r	P	n	r	P
Vertical Distance (cm)	7	86	0.45	<0.0001	66	-0.48	0.0001
Water Cover (%)	20	95	0.33	0.001	64	-0.49	0.0001
Moss Cover (%)	50	100	0.39	0.0001	65	-0.17	0.16
Mineral Cover (%)	40	90	0.32	0.003	70	-0.45	0.0002
Organic Cover (%)	20	96	0.04	0.71	66	-0.47	0.0002
Cobble Cover (%)	75	145	0.26	0.002	10	-0.26	0.43
Gravel Cover (%)	40	100	0.38	0.0001	58	0.03	0.80
Fines Cover (%)	45	100	0.04	0.72	54	-0.55	0.0001
NMS Understory Axis	0	68	0.48	0.0001	79	-0.28	0.015
BC Understory Axis	0.5	86	0.33	0.0025	62	-0.30	0.02
Canopy Cover (%)	60	39	0.33	0.04	113	-0.04	0.64
Associated Species Cover (%)	40	41	0.34	0.03	113	-0.21	0.03

TABLE 5. The abundance of *Corydalis aquae-gelidae* correlated to environmental variables: results for the biomass index. r and P values refer to Spearman rank correlations. Bray-Curtis (BC) and NMS are alternative ordination methods. Variables with significant correlations (alpha=0.05) are reported. Optima were determined by inspection of scatterplots. Generally, abundance increases to the optima (positive r), and decreases after the optima (negative r).

Variable	Optimum	<Optimum			>Optimum		
		n	r	P	n	r	P
Vertical Distance (cm)	15	107	0.23	0.02	45	-0.68	<0.0001
Horizontal Distance (cm)	40	109	0.04	0.70	44	-0.45	0.003
Water Cover (%)	30	108	0.33	0.0007	48	-0.26	0.07
Moss Cover (%)	80	136	0.36	<0.0001	26	-0.31	0.13
Mineral Cover (%)	45	96	0.43	<0.0001	60	-0.31	0.02
Organic Cover (%)	15	84	-0.03	0.81	68	-0.45	0.0003
Cobble Cover (%)	60	129	0.32	0.0003	25	-0.17	0.40
Gravel Cover (%)	35	92	0.50	<0.0001	62	-0.02	0.89
Fines Cover (%)	45	100	0.05	0.64	54	-0.55	0.0001
NMS Canopy Axis	-0.4	50	0.08	0.57	97	-0.20	0.048
NMS Understory Axis	0.5	114	0.44	<0.0001	33	-0.48	0.006
BC Understory Axis	0.55	105	0.41	<0.0001	44	-0.19	0.22
Associated Species Cover (%)	10	18	0.18	0.46	136	-0.18	0.04

to the distance to water, to the quality and texture of the substrate, and to the presence of other plants (Tables 3, 4, Figures 3-7). Several variables represented each of these four environmental factors; only the effects of the most significant variables are illustrated. Abundance peaked near the edge of the summer water levels (Figures 3, 4). *Corydalis* abundance was reduced in organic and fine-textured substrates (Figures 5, 6); substrate types became increasingly unfavorable from types GS to GX to LX (Table 3). The effect of water level varied among substrate types (Figure 6). Abundance varied with understory composition (Figure 7) and with the density of associated plants, and was weakly correlated with canopy cover (Table 4, 5).

Although substrate cover and substrate type were correlated with the water position variables,

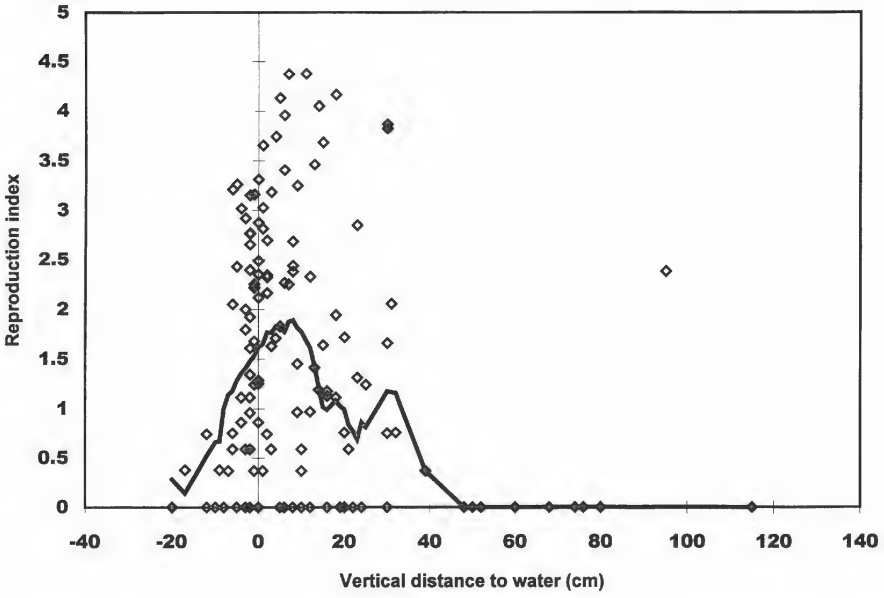

Figure 3. Relation of the vertical distance from water to the reproduction index. Many points represent more than one sample. The line is from the smoothing procedure described in the text.

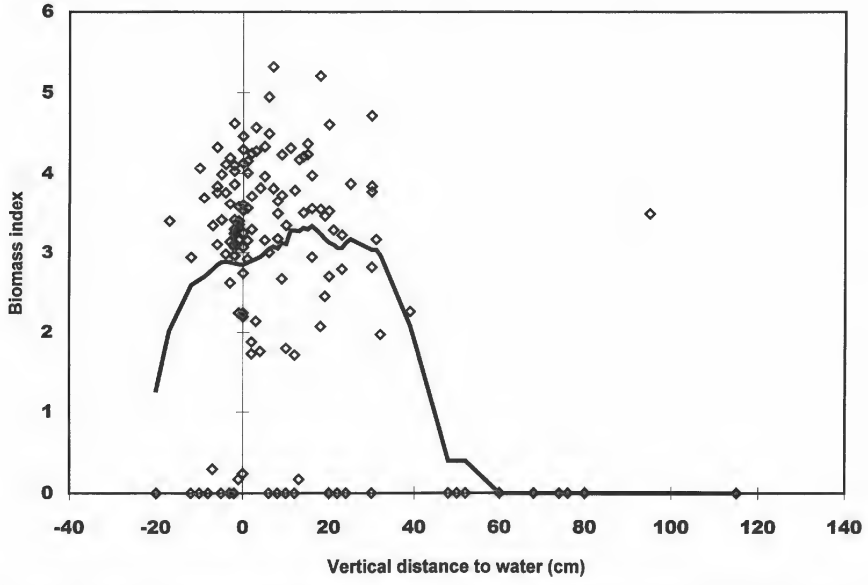

Figure 4. Relation of the vertical distance from water to the biomass index. Many points represent more than one sample. The line is from the smoothing procedure described in the text.

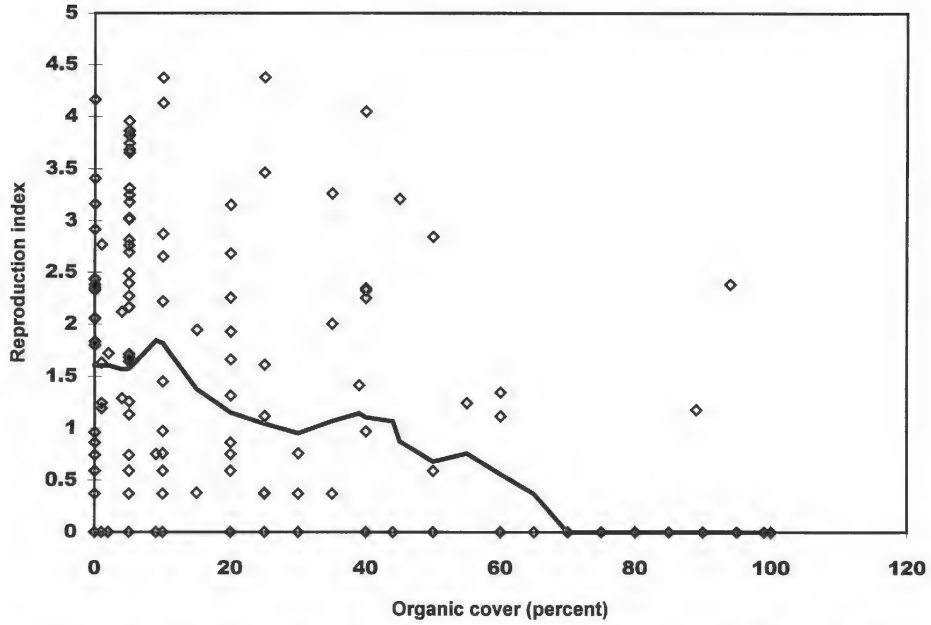

Figure 5. Relation of the cover of organic material on the plot surface to the reproduction index. Many points represent more than one sample. The line is from the smoothing procedure described in the text.

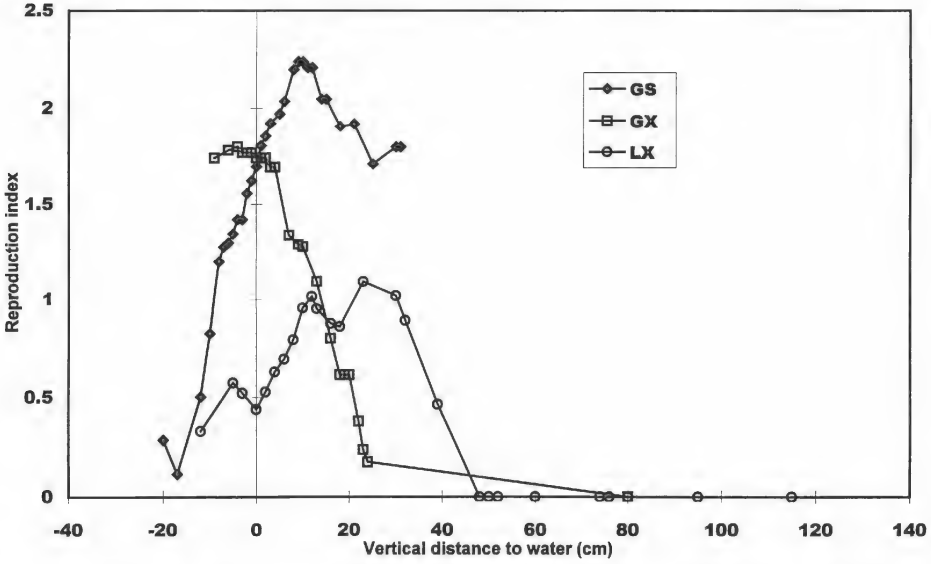

Figure 6. Relation of the vertical distance from water to the reproduction index, separating samples by substrate type. The types are GS, gravel and coarse sand, GX, gravel and sand dominant, with other materials, LX, soil or mud dominant. Associated data points are the same as the points in figure 3. The lines are from the smoothing procedure described in the text.

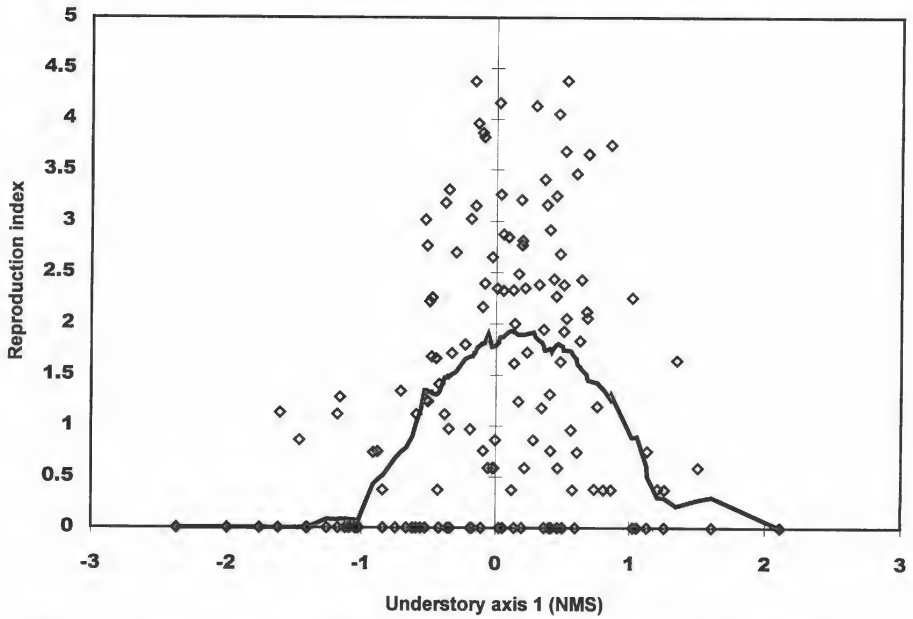

Figure 7. Relation of the first NMS understory community ordination axis to the reproduction index. Many points represent more than one sample. The line is from the smoothing procedure described in the text.

they also had an independent effect on *Corydalis aquae-gelidae*. Spearman rank correlations between the substrate cover variables, water position variables, and the abundance indices were calculated, using only the samples that were between -5 and 20 cm vertical distance to the water, the optimal range (Table 6). Within this range, the substrate cover variables were no longer significantly correlated with the water position variables, yet most remained correlated with the *Corydalis* abundance indices. The substrate types were also significantly different within this vertical range (Table 3).

Discussion

The Habitat of *Corydalis aquae-gelidae*

Corydalis aquae-gelidae grew in stream reaches with small seasonal flow fluctuations. Large

TABLE 6. Response of *Corydalis aquae-gelidae* to environmental variables where water position was optimal. Spearman rank correlations were calculated, using the 104 samples between -5 and 20 cm vertical distance to water. All correlations between the environmental variables and the vertical distance to water were not statistically significant ($P > 0.05$); no r values are given.

	Reproduction index		Biomass index		Vertical Distance
	r	P	r	P	P
Moss cover (%)	0.28	0.005	0.21	0.04	0.60
Mineral cover (%)	0.03	0.77	0.07	0.49	0.97
Organic cover (%)	-0.28	0.005	-0.29	0.004	0.54
Cobble cover (%)	0.21	0.04	0.30	0.003	0.19
Gravel cover (%)	0.11	0.28	0.12	0.21	0.66
Fines cover (%)	-0.26	0.008	-0.29	0.003	0.56

changes in flow would submerge plants in winter, and subject plants to drought in summer. In addition, high winter stream flows may physically disturb the substrate, burying or uprooting plants. *Corydalis* grew in late-successional riparian forest, mostly in areas not recently subjected to catastrophic floods. Elevational limits may have been more affected by hydrology than temperature; elevational limits coincided with the disappearance of stable stream flow regimes.

Maximum abundance occurred from 5 cm below to 20 cm above the summer water level (Figure 3), and within 40 cm horizontal distance to the nearest water surface (Table 4, 5). Optimal water cover was 10 to 30 % (Table 4, 5). The upper limit of *Corydalis* distribution along stream banks might be explained by drought, substrate differences, or a lack of the mild disturbance which could reduce competition. *Corydalis aquae-gelidae* seedlings had small root systems, with few fine roots, and died when they germinated in dry habitats (personal observation). Other plant species were denser away from the stream, which could increase soil dryness and competition. In addition, lack of cover by stream flow in the winter could allow the substrate to freeze; in cultivation, dormant plants were killed by winter substrate freezing, while plants kept indoors survived (personal observation).

Corydalis aquae-gelidae was rarely found in water deeper than 20 cm. Seedlings were only 2-4 centimeters tall, and rarely if ever survived growing completely submerged. The few adults found in swift water deeper than 20 cm grew horizontally, underwater, and appeared stunted. Substrate instability was also a problem in deeper water (personal observations).

Moss cover in *Corydalis* habitat was optimal at 50 to 80% (Table 4, 5). Low moss cover was associated with a high degree of scouring and low canopy cover. Habitats with higher moss cover were generally preferable for establishment, evidently because they were moist, only mildly disturbed, and without much litter buildup or vigorous existing herbaceous cover.

Substrates rich in organic matter, silt or clay were poor habitat for *Corydalis aquae-gelidae*. The physical properties of these substrates may account for this correlation. The bulk flow of water (as long as the substrate is fairly wet), air, and solutes decreases with smaller particle size (Hillel 1982). Coarse mineral substrates would allow faster water flow when near saturation, and faster air flow when drier. Organic matter in the less optimal soils would decrease their O2 concentration further, due to increased decomposition rates. Anaerobic processes, both chemical and biochemical, can produce substances toxic to plants, e.g., ethylene, organic acids, and ferrous sulfide (Hillel 1982), and low pH can lead to metal toxicity. Substrates rich in clays and fine organic matter have a higher capacity to hold toxic substances; greater water flow through coarser substrates would leach out these substances.

Corydalis aquae-gelidae abundance was related to plant community composition (Figure 7). Although the ordination axes provided no information for mechanistic explanations, community composition was a good indicator of habitat favorability for *Corydalis*. Species that had a response curve to the first understory axis similar to the response curve of *Corydalis aquae-gelidae* (Figure 7) include: *Epilobium glandulosum, Mimulus guttatus, Circaea alpina, Galium triflorum, Mitella ovalis, Montia sibirica,* and *Tolmiea menziesii*. These species were associated with favorable conditions for *Corydalis aquae-gelidae*, although they also grow in other conditions.

The relationships of *Corydalis aquae-gelidae* abundance to environment varied from a monotonic, nearly linear slope (Figure 5) to a complex curve (Figures 3, 7) reminiscent of the classic bell curve of niche theory (Austin et al. 1990). Aspects of this complexity included the large amount of variability, the lack of normally distributed residuals, and the interactions of the type evident in Figure 6, where the effect of water level varied depending on substrate type. The statistical methods were chosen because of the complexity of the relationships.

Management Implications

The relationships described here can be used to predict where *Corydalis aquae-gelidae* might be found during additional surveys, where it would be successful if it were to be introduced or naturally dispersed, and what effects natural or human induced environmental changes could have on its abundance. To allow persistence and regeneration of *Corydalis aquae-gelidae*, land managers should maintain canopy cover, and prevent

sedimentation or other additions of fine or organic materials to streams. Percent canopy cover had a significant effect in this study, and *Corydalis aquae-gelidae* abundance is significantly reduced in clearcuts compared to other sites; plants with no protection in clearcuts experience severe solarization, i.e., yellowed and browned leaflets (Goldenberg 1992). Clearcuts along small streams often resulted in deposition of soil and logging slash in *Corydalis* habitat (personal observations). *Corydalis* may also be damaged by stream flow reductions, increased seasonal flow fluctuations, and catastrophic floods. Hydropower projects can modify stream flow and upstream timber harvest may destabilize hydrologic conditions and contribute to sedimentation. Upstream road building and clear cuts can increase peak discharges by up to 100% (Jones and Grant 1996). Coordination of stream and forest land management activities is critical to maintain optimal habitat conditions for *Corydalis aquae-gelidae.*

Acknowledgements

Financial support was provided by a grant from the Mazama Research Committee (Portland, OR), and through personal service contracts with the Oregon Department of Agriculture and with Cascades Environmental Services (Bellingham, WA). The USDI Bureau of Land Management, Oregon State Office, covered publication costs.

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Received 7 February 1998
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The Holocene Biogeographic History of Elk (*Cervus elaphus*) in Western Washington

Abstract

Many mammalian species found today in Washington state experienced a dynamic biogeographic history during the Holocene epoch (last 10,000 years). The elk (*Cervus elaphus*) was one of those species. Seventy archaeological sites in Washington west of the crest of the Cascade Mountains have produced eighty-eight assemblages of elk remains. The oldest assemblage dates between 6000 and 7000 years ago, but most date to the last 2000 years. Documented assemblages are not a representative sample of the spatial and temporal distribution of elk as a result of how the archaeological record in western Washington has been sampled and the poor preservation of faunal materials in many sites. Available data indicate, however, that elk were widespread between 2000 and 150 years ago. Comparison of the distribution of elk between 2000 and 150 years ago to their late nineteenth and early twentieth century distribution indicates a shift in geographic range over the past 150 years. This shift is attributable to land modification and increased human predation after the middle of the nineteenth century.

Introduction

Late Pleistocene remains of bison (*Bison* sp.) and caribou (*Rangifer tarandus*) have been recovered from the northeastern portion of the Olympic Peninsula of Washington (Gustafson 1985). Remains of grizzly bear (*Ursus arctos*) apparently dating to the late Pleistocene have also been recovered from an island in the northern Puget Sound (Mustoe and Carlstad 1995). Together, these remains suggest the mammals of western Washington experienced a dynamic biogeographic history because there are no historic-period (last 200 years, as documented by Euroamerican explorers, settlers, and scientists) records for these taxa in the area (e.g., Scheffer 1946, 1995). We sought details of that history and here focus on the North American elk (*Cervus elaphus*) or wapiti.

We compiled data for the prehistoric period (> 200 years old) in an attempt to establish where elk were found in western Washington during the Holocene (last 10,000 years), to determine where they were not found, to document changes in their distribution over time, and to examine why those changes might have occurred. Although available data are insufficient to show conclusively where elk were not found prehistorically, those data indicate that elk were widespread over western Washington between about 2000 years ago and 150 years ago.

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Study Area

We define western Washington as being west of the crest of the Cascade Mountains (Figure 1). Seasonally fluctuating moisture content of sediment and the acidity of sediment created by coniferous forests characteristic of the area (Franklin and Dyrness 1973) combine to speed bone disintegration. Only sediments buffered from these environmental factors tend to contain well preserved remains of prehistoric animals (Lyman 1994). Such sediments are found in caves where they are constantly dry, or in coastal shell middens in which the calcium of the shell neutralizes sediment acidity.

Locally, climates were not stable during the Holocene and floras (e.g., Rochefort et al. 1994) and faunas (e.g., Lyman 1998 and references therein) responded to fluctuating climatic conditions throughout this epoch. During the mid-Holocene climatic interval known as the altithermal, subalpine forests in what is now Olympic National Park were more closed and timberline was higher than at present (Gallison 1994). During the early Holocene, approximately 10,000 to 5000 years ago, prairie vegetation expanded its range in the Puget Lowlands (Whitlock 1992:17). After this period, summer droughts became less intense and vegetation and climate began to take on more modern appearances (Whitlock 1992).

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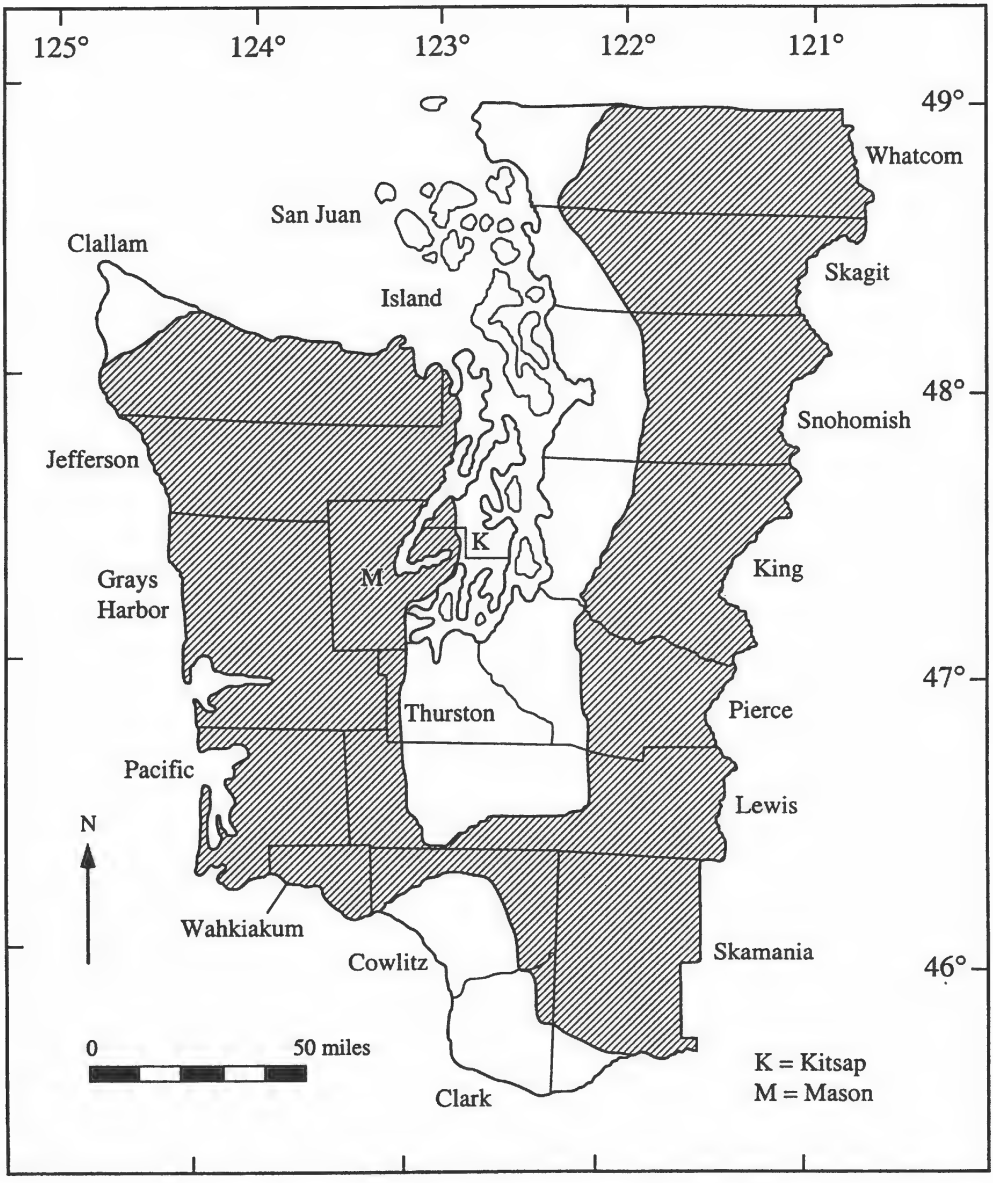

Figure 1. Modern elk distribution (shaded) in western Washington (after Booth 1947, with modifications after Ingles 1965). County lines and names shown for reference.

Studies of western Washington elk indicate this large cervid is most often found in patchy environments. The forest canopy provides thermal and escape cover, forest openings provide forage. Windstorms, landslides, and fires create openings in otherwise closed forests, creating more elk habitat (Starkey et al. 1982). Early Euroamerican explorers and settlers and late nineteenth and early twentieth century anthropologists report that Native Americans burned portions of forests to improve

production of berries, deer (*Odocoileus hemionus*), elk, and other resources (e.g., Gustafson 1983; McClure 1989; Mierendorf 1997). In conjuction with climatic change, these factors lead us to expect that elk experienced a dynamic biogeographic history during the Holocene. Climatic shifts and well-documented fire histories might be used to predict particular spatio-temporal changes in elk range, but climatic history varies across space (Mock and Bartlein 1995), as does fire history (Cwynar 1987; Dunwiddie 1986; Hemstrom and Franklin 1982). Therefore, we do not attempt to predict changes in elk distribution here and instead simply consider what the prehistoric record reveals.

Elk were distributed along both the eastern and western sides of the Cascade Mountains prior to firearm-enhanced hunting by Native Americans and European settlers. Eyewitness accounts describe an early historic abundance of elk in western Washington, and a late nineteenth and early twentieth century decline (Dalquest 1948; Scheffer 1946, 1995; Starkey et al. 1982). The approximate distribution of elk during the early twentieth century is shown in Figure 1 (Booth 1947, with modifications after Ingles 1965).

Methods

Data for this study were compiled from all known published and unpublished archaeological and paleontological reports on sites excavated in western Washington. The number of identified bones and teeth of elk per site and radiocarbon dates associated with elk remains were recorded, as were instances of stratigraphic associations of elk remains with temporally diagnostic artifacts. Elk remains modified into artifacts were not recorded as these might have been transported significant distances by prehistoric human foragers (Lyman 1994). *Assemblages* of elk remains were defined as site-specific sets of remains that were stratigraphically associated; many, but not all, of these assemblages had associated radiocarbon dates. Given the paucity of elk remains in pre-2000 yr B.P. (before present) contexts and the absence of such remains from many geographic areas, correction and calibration of dates in calendar years (Taylor 1996 and references therein) was deemed unnecessary. Several assemblages were assigned an approximate age based on associated artifact styles when those styles were of known age.

We followed Dixon and Lyman's (1996) lead and plotted elk assemblages on separate maps, one map for every 1000-year period beginning with 100–1000 yr B.P. and every thousand years prior to that period (Figure 2). The purpose of the mapping was to reveal biogeographic dynamics. This exercise was unsuccessful due to the paucity of elk remains older than 2000 years, a result of both how the zooarchaeological record has been sampled and reported and the preservational history of that record. It is therefore important to understand those factors prior to rendering interpretations of the Holocene biogeographic history of elk as indicated by prehistoric remains.

Results and Discussion

Seventy sites produced eighty-eight assemblages of elk remains. Fifty-seven assemblages from forty-six sites were assigned to a particular 1000-year period. Thirty-one assemblages with no associated styles of artifacts of known age, no associated radiocarbon dates, or multiple dates spanning multiple 1000-year periods were tallied and mapped as undated. Most assemblages date to the last 2000 years. The oldest assemblage, from Layser Cave (45LE223) in Lewis County, dates between 6000 and 7000 B.P. (Gustafson 1987). The second oldest assemblage, from the Dupont Southwest site (45PI72) in Pierce County, dates between 5000 and 6000 B.P. (Wessen 1989) (Figure 2).

The spatial distribution of sites that have produced elk remains exists not because elk were prehistorically rare in some areas and abundant in others. Rather, it is likely a function of how the archaeological record of western Washington has been sampled and preservational biases. The sample of sites producing elk remains is not spatially representative of the area as a whole because of the history of excavation. Many of the sites comprising the cluster in San Juan and Island counties were archaeologically tested in the 1950s to understand local prehistory (Bryan 1963). Many of the sites comprising the cluster in northwestern Whatcom County were excavated in the late 1960s through the early 1980s to understand local prehistory (e.g., Grabert and Griffin 1983). Sites comprising the cluster in western Clallam and Jefferson counties were excavated between 1960 and 1990 as part of a single project (Samuels and Daugherty 1991). These three clusters of sites

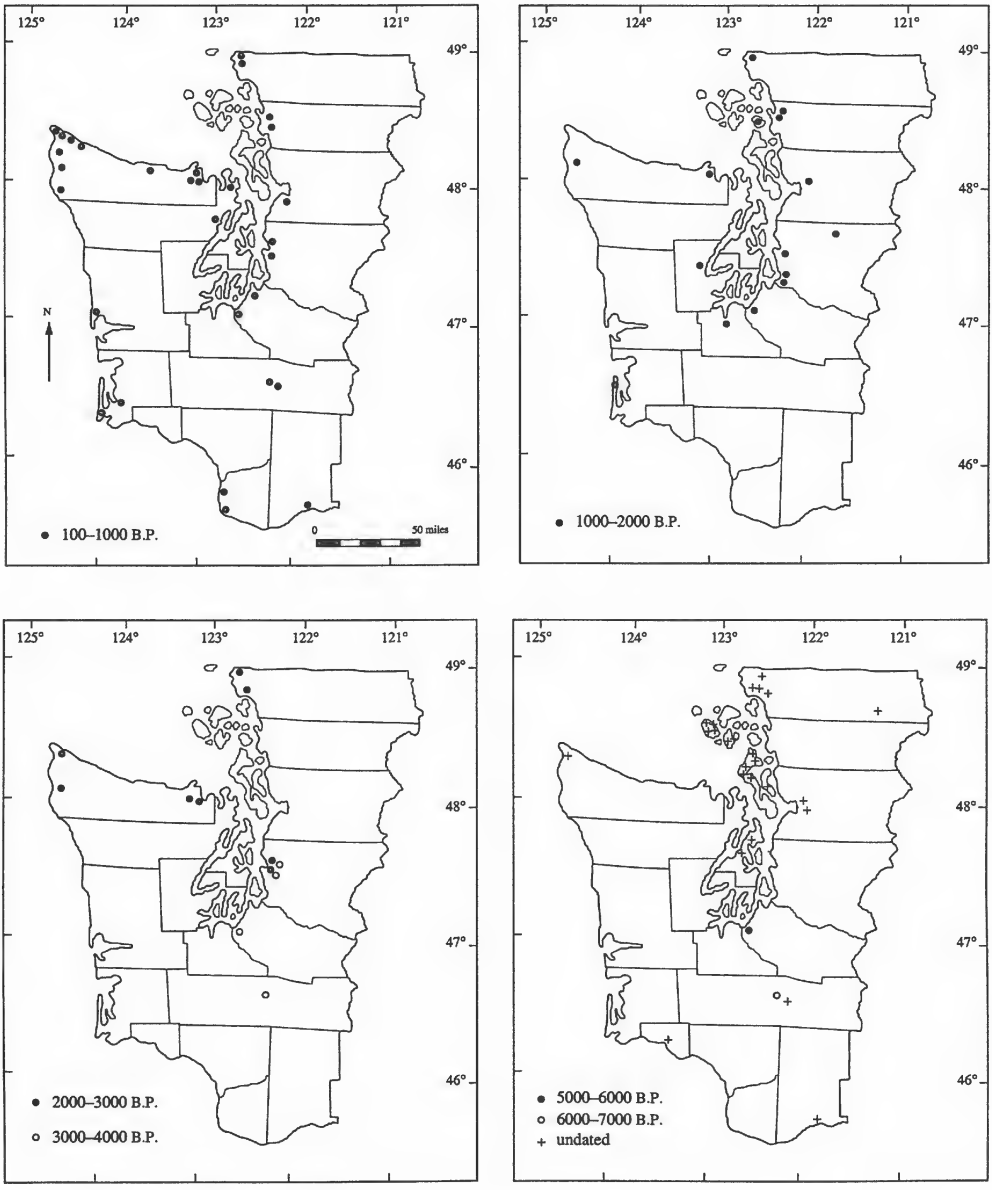

Figure 2. Distribution of archaeological sites containing elk remains per thousand-year period.

represent relatively intensive but geographically limited efforts that are not necessarily representative of western Washington. With few exceptions, the majority of the sites producing elk remains were excavated out of legal necessity rather than as the result of a research design directed toward deriving a spatially representative sample of artifacts or faunal remains.

Finally, western Washington is dominated by coniferous forest that increases the acidity of the sediment, resulting in very poor preservation of faunal remains (Lyman 1994). Poor preservation is exacerbated by seasonal fluctuations in precipitation. Sites in the interior contain elk remains if their sediments are inside caves where they are not subjected to the acid produced by conifers or to seasonal fluctuations in moisture content. Sites not in caves—typically referred to as open sites—have very poor preservational conditions precisely because they are subjected to these processes. For example, fifty-six archaeological sites within about 70 km of Mount Rainier National Park had been excavated as of mid-1994 (Lyman 1995). Twelve of these fifty-six are in caves or rockshelters, and all twelve produced faunal remains; only four of the twelve included elk remains. The other forty-four sites are open sites, and only eight of them produced faunal remains; the remains from only one of these have been reported but do not include elk remains.

In contrast to the poor preservation of faunal remains typical of open sites in interior locations, numerous mammal remains have been recovered from open coastal sites due to the presence of large amounts of mollusc shell in the site matrix. The shells provide sufficient calcium to neutralize sediment acidity and create favorable environments for the preservation of bones and teeth. This, plus the typically more intensive and extensive development and modification of the coast for human use has resulted in more coastal locations producing elk remains than interior locations.

The sample of elk assemblages is not representative of temporal patterns. In the 1950s and early 1960s, radiocarbon dating was a new procedure (Libby 1955), only a few radiocarbon dating laboratories existed, and the general consensus was that the time depth of the archaeological record in Washington state was not extensive enough to warrant such dating (Osborne 1956). For these reasons few radiocarbon dates were assayed prior to the 1970s. For example, only one of the fifteen sites sampled and reported in the 1950s and 1960s that produced elk remains was dated via radiocarbon in the 1960s. Work undertaken in the 1980s at two of those fifteen sites (45KP2 [Schalk and Rhode 1985] and 45SK7 [Robinson and Thompson 1981]) produced radiocarbon dates, but, given the published record, it is impossible to determine if the dates are stratigraphically associated with the elk remains recovered from these sites.

The Holocene archaeological record of elk in western Washington is a reasonable reflection of where elk occurred prehistorically (Figure 2), but may be a poor reflection of where elk were not found prehistorically. Recognizing these limitations, three things stand out. First, the farther back in time one goes, the less we know about the distribution of elk in western Washington. Second, elk occupied the islands of the Puget Sound, mainland coastal areas, the foothills of the Olympic Mountains and Cascade Range, and also some of the higher elevations of the interior during the last 1000 to 2000 years. And third, the distribution of elk seems to have remained relatively stable in some areas during the last several thousand years. Elk remains regularly occur in sites in western Clallam County, eastern Clallam County, western Whatcom County, and western portions of King and Pierce counties over the last 3000 to 4000 years.

Significance of Results

Comparison of Figures 1 and 2 suggests that the distribution of elk during the early twentieth century was different from that between 2000 and about 150 years ago. In fact, the two are virtually exact opposites of one another. Most prehistoric remains of elk have been recovered from coastal contexts. Undated elk remains recovered from eastern Whatcom County (Mierendorf 1997) and dated (Gustafson 1987) and undated (Lyman, unpublished data) remains from central Lewis County and north-central King County (Lyman 1988) suggest that elk inhabited these areas of the mountains prehistorically. In conjunction with what is known about bone preservation and the history of archaeological research in the area, such records suggest that the absence of elk remains in many upland or montane contexts is not a result

of the absence of elk from those areas in the past but rather is attributable to sampling and preservational biases.

Why might the historic and late prehistoric records be so different? Seventy years ago Edson (1930, 1931) and Brooks (1930) debated the cause of the lack of big game in the Mount Baker area of western Whatcom County. Brooks believed the absence of elk was part of a more general pattern as he found big game scarce over the entire region, and implied the paucity of big game was the result of hunting by Native Americans. Edson argued the rarity of big game was a result of intensive hunting by Euroamerican settlers. Similar debates, in other areas, go on today (e.g., Kay 1994; Schullery 1997). Data summarized in Figures 1 and 2 suggest a solution to such debates for the area mapped.

If Native American hunters were responsible for depletion of the elk population during the prehistoric period, then we should find progressively fewer and fewer sites plotted in Figure 2 as the maps progress from the distant to the recent past—as progressively more local populations were extirpated and hunting areas not recolonized—*if the sample is representative of the population of sites in which elk remains were deposited.* Given sample limitations for the pre-2000 B.P. periods, such cannot be perceived in the maps. But if elk populations were depleted and their range shifted accordingly as a result of hunting by Native Americans, then elk might be found historically in those areas where they were not found prehistorically. However, the available prehistoric sample indicates elk occurred virtually everywhere—recalling sampling and preservation biases—in western Washington prior to 100–150 years ago. If depletion of elk populations and concomitant range changes occurred after the arrival of Euroamerican settlers, then we should find elk historically absent from some areas where they occurred prehistorically. This is precisely what is indicated by Figures 1 and 2. And, there is a corollary that is fulfilled as well.

Elk should be historically absent from areas that were settled early by Euroamericans yet present in areas that were not densely inhabited by these early settlers. Washington (and Oregon) became a territory in 1853, just when settlements were beginning to grow quickly in number and size (Dryden 1968). Early settlers lived off the land and modified habitats with their agricultural and, particularly, logging practices. Note in particular in Figures 1 and 2 the western edge of the easternmost tier of counties. This was one of the earliest densely populated areas in the state; Bellingham (in western Whatcom County) was established in 1852, Everett (in western Snohomish County) in 1862, and Seattle (in western King County) in 1851. Numerous prehistoric occurrences of elk are known in these areas, but Booth (1947) listed no historic records of elk there. Western Clallam County and the Portland Basin, including Clark County, historically lack elk where they were found prehistorically. The last, too, was settled early and densely; Portland (south of and across the Columbia River from Clark County) was established in 1844 and Fort Vancouver (in southwestern Clark County) in 1825. In his journals of 1825, David Douglas (1914:155) wrote of the Portland Basin that elk were "plentiful in all the wooded parts of the country." Apparently this was not the case one hundred years later when Booth (1947) compiled his data.

Logging was a major industry throughout the settled portions of western Washington, and although this may have produced more elk habitat, subsistence hunting by early Euroamerican settlers seems to have outweighed the benefits and resident elk populations were decimated. Schullery (1984) suggests some firearms made their way over the crest of the Cascade Range prior to the first major waves of Euroamerican settlers. The impact of firearm-equipped Native Americans on local elk populations is impossible to estimate, but such may have initiated decreases in some local populations prior to the arrival of Euroamericans and contributed to their demise afterwards. We suggest it is doubtful that the impact was geographically universal because local Native American populations were, in the middle of the nineteenth century, less than half the size they had been a century earlier as a result of the introduction of European diseases for which Native Americans had no natural immunity (e.g., Black 1992; Meltzer 1992). Finer temporal resolution in conjunction with more and larger samples of elk remains can be used to test this suggestion.

Conclusions

Prehistoric remains of elk have been reported in areas of western Washington where numerous archaeological sites have been excavated but not in areas where little excavation has been undertaken.

This bias is exacerbated by the general lack of preservation of faunal remains in archaeological sediments underlying local coniferous forests and the paucity of radiocarbon dates associated with those remains. Nonetheless, the available data suggest elk were widespread over much of western Washington at least during the last half of the Holocene, particularly between 2000 and about 150 years ago. Comparison of the prehistoric record of elk in western Washington with the historic record for this species suggests that during the last half of the nineteenth century the distribution of elk shifted as a result of land modification associated with Euroamerican settlement and depletion by human predation.

Acknowledgements

For help in obtaining obscure reports, we thank Kenneth M. Ames, Sarah K. Campbell, Laura S. Phillips, Julie K. Stein, and Rob Whitlam. Information on various sites and excavations was provided by Astrida Blukis Onat, Gail Thompson, Robert Mierendorf, and Linda N. Goetz. We thank Steve Wolverton and three anonymous reviewers for comments on an early draft, and Dan Glover for preparing the figures. This research was funded in part by the McNair Scholars Program at the University of Missouri.

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Received 18 May 1998
Accepted 12 March 1999

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Temporal Variation in Prey Consumed by Big Brown Bats (*Eptesicus fuscus*) in a Maternity Colony

Abstract

We hypothesized that prey consumed by bats in maternity colonies differed by season and perhaps by time of day during postnatal development of young. Such was based on information that availability of prey to aerial-foraging bats differs spatially and temporally, some bats are selective of prey, and activity of lactating females varies with stage of development of young and their demands for energy. We identified prey in fecal samples collected at 2400 and 0600 h at weekly intervals from beneath two clusters of big brown bats (*Eptesicus fuscus*) in a maternity colony in a barn in Benton County, Oregon during postnatal development of young. Only consumption of moths (Lepidoptera) differed significantly by week; neither percent frequency nor average percent volume for any taxon of prey differed significantly by time of day. The overwhelming preponderance of caddisflies (Trichoptera) consumed possibly obscured variation in frequency and volume of other taxa of prey eaten. A maternity colony more distant from a single abundant, highly desirable, source of easily captured prey possibly would exhibit greater differences in prey consumed during postnatal development of young.

Introduction

In most regions, including Oregon where our study was conducted, beetles (Coleoptera) are considered the primary prey of big brown bats (*Eptesicus fuscus*), whereas moths (Lepidoptera) usually are not eaten or constitute only a small portion of the prey consumed (Hamilton 1933; Phillips 1966; Ross 1967; Whitaker 1972; Black 1972, 1974; Whitaker et al. 1977, 1981; Henny et al. 1982; Brigham and Saunders 1990). An exception is in British Columbia, where prey consumed by this bat was largely flies (Diptera) and caddisflies (Trichoptera; Brigham 1990). Nevertheless, essentially all of these studies were conducted with little regard to season, time of day, foraging behavior, or life-history events that possibly impact either availability of various prey or energetic demands of the bats. In Indiana, however, where beetles composed 48.6-85.0% of the prey consumed by *E. fuscus* in several colonies, the contribution of major insect groups consumed by the species in one colony where guano was sampled at 1-2-week intervals differed significantly at various times during late spring and summer (Whitaker 1995). Also, Whitaker et al. (1996) found significant differences in proportions and frequencies of several prey species consumed by Mexican free-tailed bats (*Tadarida brasiliensis*) during evening and pre-dawn foraging bouts in an 8-day period.

Availability of various prey to aerial-foraging bats differs spatially and temporally (Denno and Dingle 1981; Aldridge and Rautenbach 1987; Brigham 1990; Brigham and Saunders 1990); some bats are selective of available prey on the basis of size and perhaps other characteristics (Barclay 1985; Fenton 1990; Whitaker 1994); and lactating bats spend the least time in torpor (Audet and Fenton 1988), exhibit the greatest demands for energy (Kurta et al. 1989, 1990), and alter their foraging behavior in response to development of young (Davis et al. 1968). These features suggest that bats in maternity colonies during the period of postnatal development of young possibly consume different proportions of various taxa of prey either actively (and selectively) in reponse to the increasing energy demands of young (Kurta et al. 1989), or passively because of variation in availability of prey diurnally, seasonally, and spatially.

We hypothesized that before young are capable of foraging flights (about 4 weeks of age; van Zyll de Jong 1985), prey consumed by lactating females might vary temporally. Such might occur if the females shifted foraging areas or times in response to their changing nutritional needs

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and those of their offspring or in response to differences in availability of various taxa of prey. To assess variation in prey consumed, we analyzed fecal samples collected at midnight and early morning at weekly intervals from beneath two clusters in a maternity colony while young were being reared.

Methods

Fecal pellets produced by big brown bats in a maternity colony located in the loft of a two-story barn near Fairplay School approximately 3.2 km north of Corvallis, Benton Co., Oregon were collected. The barn, owned by Oregon State University, is used for storage; human activity there is infrequent. The bats occurred in two clusters about 10 m apart; they occupied spaces between strippings and rafters near the ridgepole of the barn. Piles of accumulated guano on the floor were evidence of the precise location of the roosts; the piles were removed the afternoon before collection of samples commenced. The guano piles contained several newly fallen dead neonates indicating that parturition in the colony was ongoing.

A piece of white bed sheet marked with 32 (4 by 8) 25-cm, numbered squares and with 3.8-cm wooden slats attached to each end, was spread on the plywood floor directly beneath each cluster at 1800 h each evening. Samples were collected at 2400 h and again at 0600 h the following morning. The sheets were cleaned and repositioned after each midnight collection, then removed after each early morning collection. Sampling was repeated at 7-day intervals from 1 to 23 July 1995. A random-numbers generator was used to determine the squares from which fecal pellets were collected. For each cluster, two fecal pellets were selected from each of 12 squares plus one pellet from a 13th square for a total of 25 pellets at each sampling period. Each pellet was placed in a labeled envelope and the envelope sealed. A flashlight, always directed toward the floor, was the only light used; we also collected samples quickly to avoid disturbing the bats more than necessary.

Each fecal pellet was placed in a Syracuse watch glass with sufficient water to cover the prey fragments after the pellet was teased apart. Prey taxa contained therein were identified and the proportion of each estimated visually (Whitaker 1988). Data were summarized by average percent volume and percent frequency. Multivariate analysis of variance followed by Fisher's least-significant difference tests were used with arcsine-transformed data to test for significant differences among clusters, time of day, and week of collection for each of the seven orders of insects preyed upon most. STATGRAPHICS Plus Version 2.1 for Windows was used for the statistical tests; 0.05 probability was accepted as significant.

Results

Eleven orders of insects plus mites (Acarina) and spiders (Araneae) were identified in the fecal pellets (Figure 1). In all collections, caddisflies occurred most frequently and contributed most to the volume of prey remains in the feces from the bats. Beetles usually ranked second in both percent frequency and average percent volume, and commonly were followed by moths, true bugs (Hemiptera), and flies. However, the rank in percent frequency or average percent volume of no taxon other than caddisflies was consistent among collections (Figure 1). Of the beetles, June bugs (Scarabaeidae) occurred in 115 (28.8%) samples and composed 10.7% of the volume of prey remains; unidentified beetles occurred in 103 (25.8%) samples and composed 5.9% of the volume of prey remains. Other families of beetles identified (followed parenthetically by percent frequency and average percent volume) were Carabidae (ground beetles; 1.25, 0.6), Curculionidae (snout beetles; 1.5, 0.2), Dytiscidae (predaceous diving beetles; 0.5, 0.1), Alleculidae (comb-clawed bark beetles; 0.25, 0.06), Cerambycidae (long-horned beetles; 0.25, 0.05), and Chrysomelidae (leaf beetles; 0.25, 0.1). Most flies were not identified to family (12.0, 1.7), but Culicidae (mosquitos; 0.75, 0.1), Chironomidae (midges; 0.75, 0.04), and Tipulidae (craneflies; 0.25, 0.05) were identified. Conversely, most hemipterans were identified to families Corixidae (water-boatmen; 10.25, 2.1), Pentatomidae (stinkbugs; 0.05, 0.2), and Miridae (leaf bugs; 0.25, 0.05); relatively few were not identified to family (3.25, 0.5). Orthoptera consisted entirely of Gryllidae (crickets; 5.5, 2.9). Hymenoptera was represented by Formicidae (ants; 1.25, 0.2), Ichneumonidae (ichneumons; 2.75, 0.5), and unidentified taxa (0.25, 0.04); Homoptera included Cicadellidae (leaf hoppers; 2.0, 0.4), Delphacidae (delphacid planthoppers; 0.25, 0.01), and unidentified taxa (0.25, 0.01). The other three orders of insects, insects not identified to order,

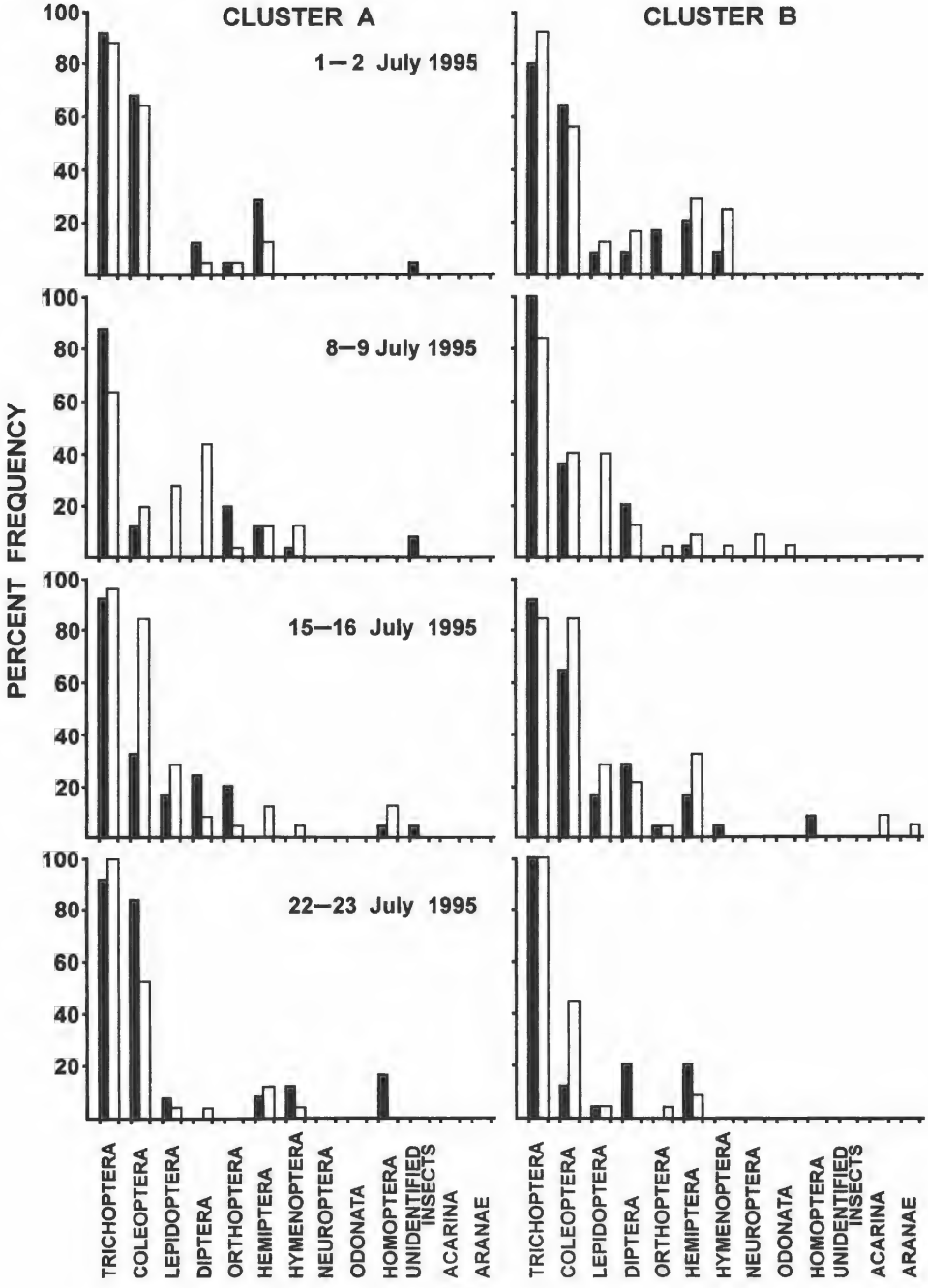
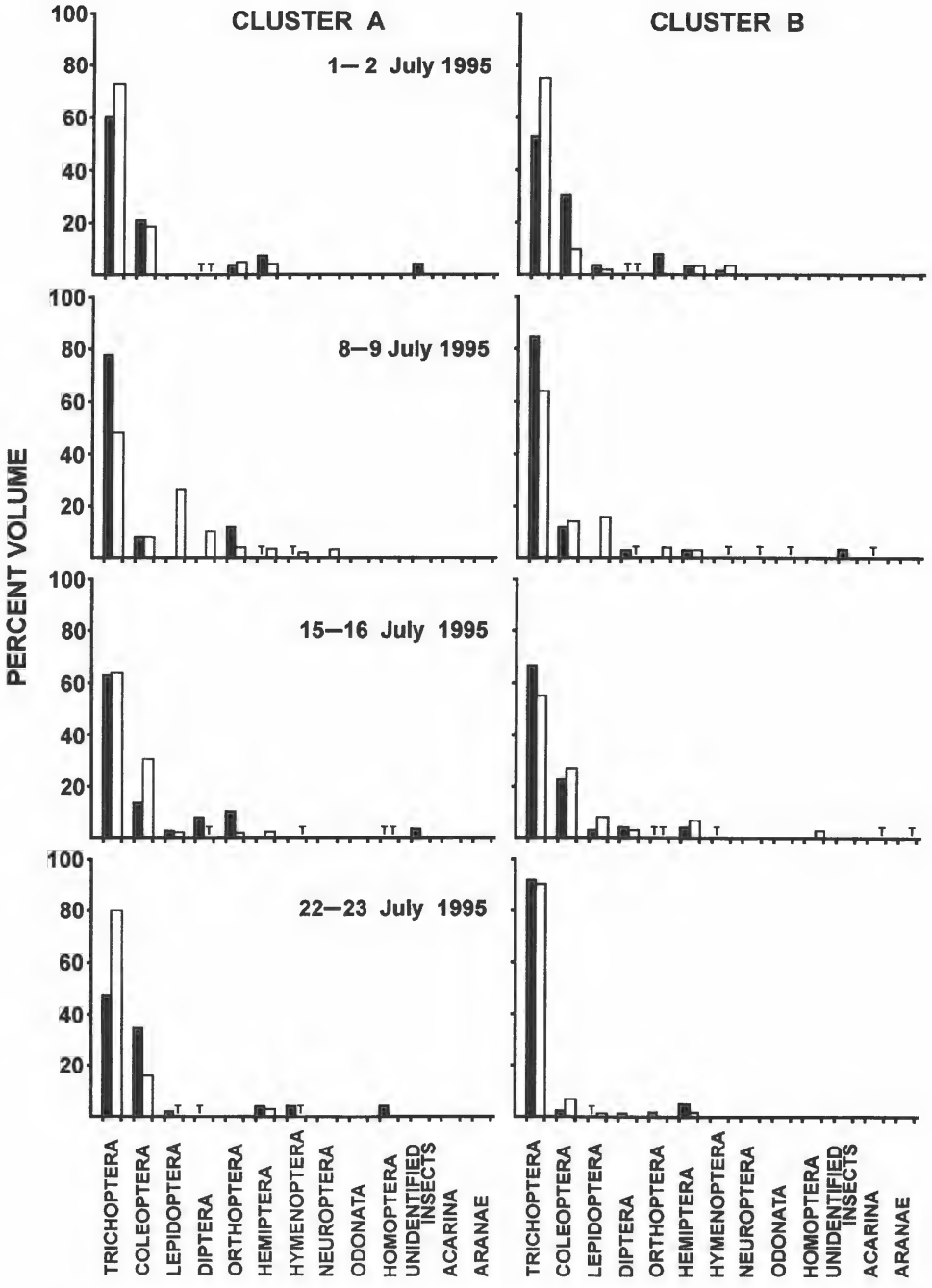


Figure 1. Percent frequency and average percent volume of 10 orders of insects, unidentified insects, Acarina, and Araneae in 1-23 July 1995. Samples of pellets deposited between 1800 h and 2400 h are represented by solid bars and those of



fecal pellets collected at weekly intervals beneath two clusters in a maternity colony of *Eptesicus fuscus* in Benton Co., Oregon, pellets deposited between 2400 h and 0600 h are represented by open bars; "T" indicates values <1%.

Acarina, and Araneae were rare and contributed little to the diet of big brown bats (Figure 1).

When all variables (cluster, week of collection, and time of day) were considered simultaneously, percent frequency and average percent volume of moths were significantly greater in collections made during weeks 2 and 3 than during weeks 1 and 4. These were the only significant differences observed with multivariate analysis of variance (Table 1). However, Fisher's least-significant difference test indicated homogenous groups by week of collection within clusters A and B (Figure 1) were significantly different in percent frequency between clusters for beetles (A: weeks 1, 3, and 4; B: weeks 1, 2, and 4), hemipterans (A: weeks 2, 3, and 4; B: weeks 1, 3, and 4), and caddisflies (A: weeks 3 and 4; B: weeks 1, 2, and 3). No similar groupings were observed in average percent volume by week of collection.

Discussion

Prey consumed by big brown bats in the maternity colony from which we obtained fecal pellets differed greatly from that reported for the species throughout most of its range north of Mexico (Hamilton 1933; Phillips 1966; Ross 1967; Black 1972, 1974; Brigham and Saunders 1990; Whitaker 1972, 1995), including Oregon (Henny et al. 1982; Whitaker et al. 1977, 1981). An exception was along the Okanagan River, British Columbia, where caddisflies also constituted a major component (61.6-65.3%) of prey items identified (Brigham 1990). We suspect that our findings are similar to those of Brigham (1990) because our colony was located only 0.8 km west of the Willamette River. At dusk in summer, mating flights of caddisflies frequently were observed along the river. The preponderance of caddisflies and other taxa associated with aquatic environments (Dytiscidae, Culicidae, Chironomidae, Corixidae) among prey remains suggests that the river served as a major foraging area for bats in the maternity colony. The proximity to water of collections of samples for previous dietary analyses of big brown bats in Oregon was either not described (Whitaker et al. 1977, 1981) or samples were obtained from specimens collected over ponds (Henny et al. 1982).

Greater percent frequency and average percent volume of moths and the lesser percent frequency of hemipterans preyed upon during weeks 2 and 3, and the relatively low percent frequency of beetles consumed during week 2 (Figure 1) possibly indicate changes in foraging behavior, habitats, or timing, or in availability of prey during development of young. Neither percent frequency nor average percent volume were significantly different for any taxon of prey between midnight and morning collections, but more moths occurred in fecal samples collected in the morning and more hemipterans occurred in midnight samples (Figure 1). Although we cannot exclude the possibility of temporal variation in prey selectivity by the bats, these differences more likely are a reflection of changes in relative abundance of these taxa of prey within a foraging area temporally or

TABLE 1. Results of multivariate analyses of variance of arcsin-transformed percent frequency of occurrence and average percent volume by cluster, date of collection, and time of day for the seven most common orders of insects consumed by big brown bats in a maternity colony in Oregon, July 1995. Values in bold are significant.

Order of insects	Percent volume						Percent frequency					
	Cluster[a]		Date[b]		Time[a]		Cluster[a]		Date[b]		Time[a]	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Trichoptera	1.60	0.23	1.03	0.42	0.01	0.93	0.66	0.44	2.46	0.12	0.24	0.64
Coleoptera	0.48	0.51	0.96	0.45	0.07	0.80	0.08	0.79	2.50	0.12	0.60	0.46
Lepidoptera	0.20	0.67	**12.26**	**0.01**	0.08	0.79	0.25	0.64	**12.54**	**0.01**	1.97	0.21
Diptera	2.18	0.18	1.39	0.32	0.66	0.44	0.03	0.88	1.32	0.34	0.50	0.50
Orthoptera	0.93	0.38	0.80	0.54	4.47	0.09	0.27	0.62	0.23	0.87	4.87	0.08
Hemiptera	1.28	0.29	1.30	0.34	0.60	0.46	0.47	0.51	2.53	0.12	0.00	0.95
Hymenoptera	0.00	0.99	0.81	0.57	0.01	0.93	0.07	0.81	0.85	0.55	0.32	0.61

[a] *d.f.* = 1
[b] *d.f.* = 3

that adult females were foraging in different areas at different times of the night. The increase in consumption of moths, usually an uncommon prey of *E. fuscus*, tends to support our contention that observed differences were not related to temporal variation in prey selectivity by the bats. Also, differences in weekly homogenous groups between clusters suggest that bats composing the two clusters may have foraged in different areas at times.

As energetic demands of young increase with age, adult females possibly spent more time foraging over agricultural fields and along wooded areas that lay between the barn housing the colony and the river. Such would be consistent with optimal foraging theory in that maternal females would forage closer to the colony and possibly spend less time in foraging. Foraging over agricultural fields and along wooded areas also would be consistent with the increase in moths preyed upon during weeks 2 and 3 of our study. Nevertheless, the overwhelming preponderance of caddisflies in all 16 samples (Figure 1) suggests that maternal females continued to use the nearby riverine area as a major foraging area. This, in turn, suggests that what might have been even greater temporal differences in other taxa of prey consumed likely were obscured by the greater consumption of the presumably abundant and easily available caddisflies. We speculate that similar sampling of feces produced by big brown bats in a maternity colony remote from a single abundant source of easily captured prey possibly would reveal greater temporal variation in prey consumed during development of young.

Acknowledgements

We thank J. P. Hayes and K. T. Wilkins for comments on an earlier draft of the manuscript. This is Oregon Agricultural Experiment Station Publication no. 11,205.

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Received 18 March 1998
Accepted 10 April 1999

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Detecting Long-Term Hydrological Patterns at Crater Lake, Oregon

Abstract

Tree-ring chronologies for mountain hemlock (*Tsuga mertensiana*) were used to reconstruct the water level of Crater Lake, a high-elevation lake in the southern Cascade Range of Oregon. Reconstructions indicate that lake level since the late 1980s has been lower than at any point in the last 300 years except the early 1930s to mid 1940s. Lake level was consistently higher during the Little Ice Age than during the late 20th century; during the late 17th century, lake level was up to 9 m higher than recent (1980s and 1990s) low levels, which is consistent with paleoclimatic reconstructions of regional precipitation and atmospheric pressure. Furthermore, instrumental data available for the 20th century suggest that there are strong teleconnections among atmospheric circulation (e.g., Pacific Decadal Oscillation), tree growth, and hydrology in southern Oregon. Crater Lake is sensitive to interannual, interdecadal and intercentenary variation in precipitation and atmospheric circulation, and can be expected to track both short-term and long-term variation in regional climatic patterns that may occur in the future.

Introduction

The time series of annual growth stored in tree rings is a repository of information on regional climate, as well as on local forest productivity. Dendrochronological techniques have proven particularly useful in reconstructing past hydrological variation by quantifying the relationship among interannual variation in climate, variation in hydrological parameters (e.g., streamflow) and radial tree growth (Meko et al., 1980, Cook and Jacoby 1983, Blasing and Duvick 1984, Meko and Stockton 1985, Landwehr and Matalas 1986, Brinkman 1987, 1989, 1992, Michaelsen et al. 1987, Robertson and Josza 1988, Stahle et al. 1988, Loaiciga et al. 1992, 1993, Stahle and Cleaveland 1993, Woodhouse 1993, Young 1994, Shen and Tabois 1995). These reconstructions quantify long-term trends and expected variation in hydrological systems associated with regional climate, and provide valuable input to policy decisions about water consumption and allocation (Stockton 1990).

Reconstructing the water level of lakes can be challenging, because most lakes comprise only a small fraction of the surface area in a watershed. Lakes frequently have unknown inputs from inflow streams, unknown losses to groundwater and outflow streams and complex evaporative relationships with the atmosphere. Crater Lake, a deep, high-elevation lake located in the southern Cascade Range of Oregon (Drake et al. 1990), is a notable exception to this generalization. The surface area of Crater Lake comprises 78.5% of its watershed surface area, and there are no streams flowing into or out of the lake. Because Crater Lake comprises such a large proportion of its watershed, water level is very responsive to interannual variation in precipitation (Redmond 1990, Nathenson 1992), giving the lake its reputation as "the world's largest rain gauge" (Larson 1990), despite the fact that there is some "leakage" due to seepage.

In this study, we used climatically-sensitive tree-ring chronologies and climatic and hydrological records from the 20th century to reconstruct annual precipitation and water level at Crater Lake. We quantified the rate of change in water levels since the late 1600s, which includes much of the Little Ice Age (ca. 1600-1850), a period with cooler climate in western North America (Fritts and Lough 1985, Graumlich and Brubaker 1986, Folland et al. 1990, Briffa et al. 1992). Knowledge about past water levels of lakes (prior to measurement records) is valuable for understanding hydrological variation at different temporal scales (Stine 1990, 1994) and can improve

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predictions of how hydrological systems in the Pacific Northwest may respond to various climatic conditions in the future.

Methods

Research was conducted in Crater Lake National Park in the southern Cascade Range of Oregon (Fig. 1). Crater Lake is a deep hyperoligotrophic lake that covers the floor of Mt. Mazama caldera which formed ca. 6,800 B.P. The average elevation of the lake is 1,882 m. Area of the water surface is 53.2 km^2, and the drainage basin is 67.8 km^2 (Redmond 1990, Nathenson 1992). As previously noted, the lake occupies 78.5% of its own drainage basin. Lake volume is 17.3 km^3, with maximum depth of 589 m (Collier et al. 1990). Steep walls form a high rim (elevation ca. 2,100 m) around the lake, inflowing waters originate within the caldera and there is no surface outlet. The only ways for water to leave the basin are through seepage and evaporation. Seepage is

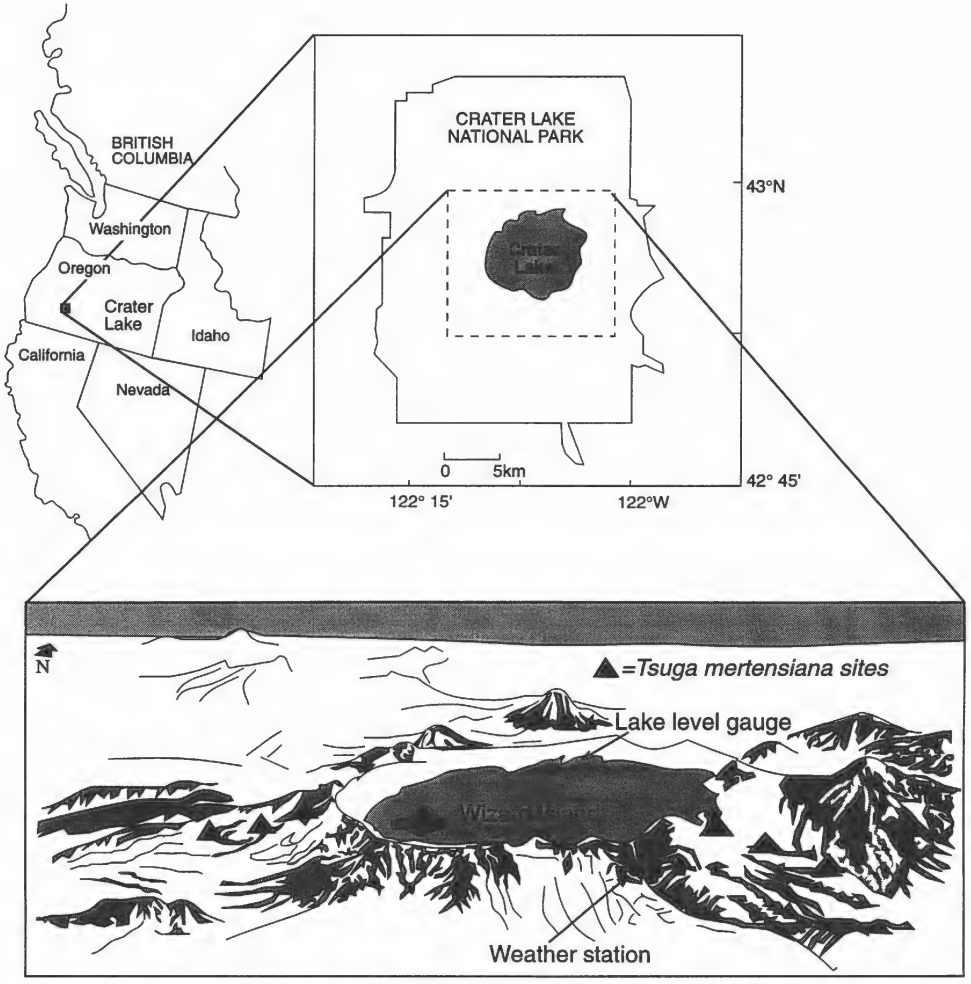

Figure 1. Location of Crater Lake in Crater Lake National Park, southern Cascade Range, Oregon. The weather station, lake-level gauging station and mountain hemlock (*Tsuga mertensiana*) sampling sites are indicated.

approximately 0.35 cm/day (128 cm/yr) and does not appear to vary with lake level, while evaporation is approximately 0.33 cm/day (120 cm/yr) (Redmond 1990, Nathenson 1992).

Monthly total precipitation and mean air temperature data for Crater Lake (measured at Crater Lake National Park headquarters, elevation 1,973 m) are available since 1931. Mean annual precipitation at Park headquarters is 171 cm, of which 80-90% falls as snow during the winter (October through April); mean annual snowfall (in solid form) is 1,314 cm (Redmond 1990). Mean annual temperature (1961-1990) is 3.1°C, with a mean annual minimum of -2.9°C and mean annual maximum of 8.9°C. Lake level has been measured since 1908; since 1961, data have been recorded at a permanent gauge located on the west side of the lake, although measurements prior to this time are also considered to be accurate (Redmond 1990).

Tree-ring chronologies were developed for mountain hemlock (*Tsuga mertensiana*) at each of 7 sites in Crater Lake National Park. Mountain hemlock is the dominant tree species throughout much of the region adjacent to the rim of the lake. Shasta red fir (*Abies magnifica* var. *shastensis*) is codominant at some sites, especially at lower elevations. Sites were located along an elevational gradient on the western side (3 sites) and eastern side (3 sites) of the lake, and on Wizard Island (1 site) within the lake basin (Fig. 1). Tree age at 1 m height was up to 439 years (Table 1). Twenty trees from each site were cored with increment borers at 1 m above the ground; only larger (and presumably older) trees without visible injury to the crown and bole were sampled. Two cores were extracted per tree, of which one core was analyzed. Tree cores were sanded and crossdated (Fritts 1976), and ring widths were measured to the nearest 0.01 mm in the laboratory.

Tree-ring chronologies were calculated (through standardization) with the program ARSTAN (Holmes 1984) using a stiff cubic smoothing spline with a 50% frequency response cutoff of 200 years (Cook and Peters 1981, Holmes 1983) applied to the ring-width series of each tree. The ring width for each year in the series was divided by the spline value to give a time series of index values. An autoregressive model was fit to each index, and the residual series for all trees in a stand were averaged to give a site chronology. More flexible smoothing splines (50% frequency response cutoff of 25, 50 and 100 years) were tested to determine the potential impact of standardization on reconstructions of precipitation and lake level. These other curve-fits had minimal effect on the chronologies or ultimate reconstructions, so we retained the stiffer spline which would tend to retain low-frequency variance in the calculated chronologies.

Correlation analysis was used to determine the relationship between annual tree growth and monthly and annual precipitation (based on hydrological years, October through September). The period of concurrent tree-growth and climatic data used in the analysis was 1931 through 1991.

Principal component analysis (PCA) was conducted on the 7 site chronologies as well as the chronologies lagged forward 1 year (total of 14 variables in the PCA). PCA is commonly used to define the common variance among chronologies

TABLE 1. Summary of characteristics of sampled mountain hemlock (*Tsuga mertensiana*) in Crater Lake National Park. Trees on the western and eastern rim of the lake (20 trees per site) were sampled across an elevational gradient (high, mid, low); only one site was sampled on Wizard Island.

			Earliest year in chronology		Chronology statistics		
Site	Elevation (m)	Mean diameter (cm, ±1SD)	Mean (yr, ±1SD)	Range (calendar yr)	Mean sensitivity	Auto-correlation	Common variance (%)
West - high	2200	82.6 (14.1)	1715 (57)	1607-1787	0.201	-0.061	52.0
West - mid	2060	70.8 (10.8)	1745 (36)	1687-1809	0.230	0.052	50.7
West - low	1940	66.7 (14.1)	1757 (68)	1597-1856	0.173	0.193	44.0
East - high	2290	89.5 (20.2)	1766 (64)	1641-1889	0.196	0.076	49.4
East - mid	2060	73.6 (9.6)	1796 (49)	1640-1887	0.193	0.208	56.8
East - low	1900	61.6 (12.7)	1736 (60)	1576-1833	0.144	0.215	41.8
Wizard Island	2000	58.6 (11.5)	1726 (83)	1553-1856	0.189	0.157	41.6

(Graumlich 1993), reduce the number of variables used in regression and reduce multicollinearity between variables (Graumlich 1987, Loaiciga et al. 1993, Peterson et al. 1993). PCA was conducted for the entire time series of tree growth, and 6 principal components (PCs) since 1931 (when climatic data are available) were included in a stepwise regression procedure to predict annual precipitation change. The PCs were not rotated. Coefficients of determination (r^2) were calculated for the regression model. Observations were left out of the regression model one at a time (one-fold cross-validation) (Graumlich 1987, Michaelsen et al. 1987, Michaelsen 1988, Loaiciga et al. 1993) to determine predictive power, and reconstructions were developed back to 1687, the point at which tree-growth data are available for a total of 25 trees and all 7 sampling sites are represented in the data set. Although this is subjective, the variance properties of the reconstructions did not seem to be affected much by sample size moving forward in the time series from this point. Residuals from the regression were examined for departure from a normal distribution with the Shapiro-Wilk statistic, and autocorrelation structure was tested with the Durbin-Watson statistic.

An identical procedure was used to develop a regression model with 4 PCs relating tree-ring chronologies (growth indices) to annual changes in lake level since 1908 (when lake-level data are available). Absolute lake levels over time were calculated from the reconstructed changes in lake level.

Results and Discussion

Annual tree growth is negatively correlated with precipitation during winter prior to the current growing season (Fig. 2), indicating that growth of *T. mertensiana* is enhanced by a longer snow-free period and reduced by deep snowpacks that

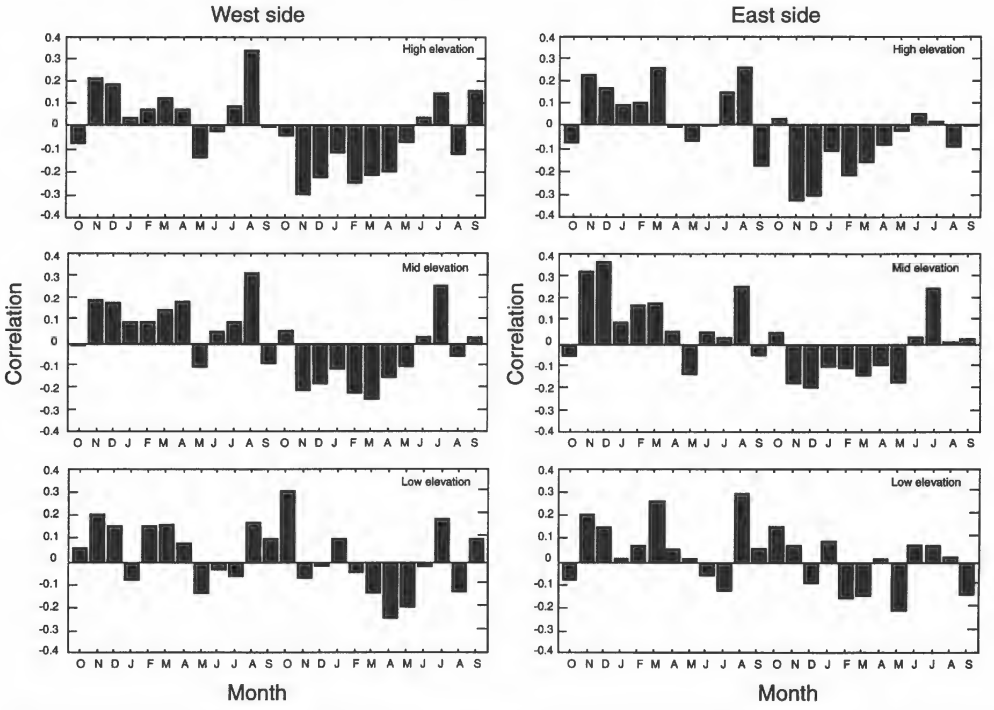

Figure 2. Correlations of annual tree-growth index with precipitation for the current (year *t*) and previous (year *t-1*) hydrological year (October through September, 1931-1991) are shown for 6 mountain hemlock (*Tsuga mertensiana*) sites in Crater Lake National Park. Although it is possible to calculate significance levels for the correlations, alpha levels could be inflated by potential between-month intercorrelation of the growth-climate relationship. Correlations for Wizard Island trees (not shown) are similar to those for the west-side, low-elevation site.

extend into the summer. This climate-growth relationship is similar to that found for *T. mertensiana* at other sites (Graumlich 1987, Peterson and Peterson in review) and for other subalpine conifer species in the Pacific Northwest (Peterson and Peterson 1994, Ettl and Peterson 1995a,b, Peterson 1998, Smith and Laroque 1998) and the Rocky Mountains (Colenutt and Luckman 1991, Villalba et al. 1994; although growth of these species has an equal or greater positive correlation with summer temperature). Correlations for winter precipitation are greater for higher elevation sites located near the rim of the Crater Lake caldera (Fig. 2). These sites generally begin to accumulate snowpack in late October, have a peak snowpack of >300 cm in April, and reach complete snowmelt by early July (Redmond 1990). Growth is enhanced by winter precipitation during the previous year (positive correlation) (Fig. 2) because of the effect of high snowfall on long-term soil moisture storage (Peterson and Peterson 1994, Ettl and Peterson 1995b). August precipitation during the previous year also has a positive correlation with growth.

In addition, growth is positively correlated with current-year spring and early summer temperatures, indicating that growth is enhanced by warm temperatures favorable for photosynthesis and early snowmelt (Peterson and Peterson in review). Growth may be reduced by high temperatures during the previous summer (negative correlation) because of the impacts of low soil moisture on carbohydrate storage (Ettl and Peterson 1995b).

The first 6 PCs derived from PCA, which account for 88% of the variance in the data (of which the first two PCs account for 75%), were retained in the stepwise regression procedure for predicting annual precipitation. Regression of precipitation on these PCs results in a significant model (r^2=0.46, $p<0.001$). The correlation between the reconstructed value of the deleted observation and actual precipitation is 0.60 ($p<0.001$). Residuals from the regression show no significant autocorrelation (first-order autocorrelation=0.03, Durbin-Watson statistic=2.06) or departure from a normal distribution.

Using the same analytical approach, regression of lake-level change on PCs 1, 3, 5, and 6 results in a significant model (r^2=0.40, $p<0.001$). Cross-validation indicates that the correlation between the reconstructed value of the deleted observation and the actual change in lake level is 0.57 ($p<0.001$). Residuals from the regression contain some serial correlation (first-order autocorrelation=0.14, Durbin-Watson statistic=1.70), and the distribution of residuals departs from normal in the shortness of the tails (low kurtosis, $p<0.05$).

Because precipitation is so strongly correlated with lake-level change at Crater Lake, (Redmond 1990), our analyses focus on the quantitative relationship of tree growth, precipitation (most of which falls as snow) and lake level. Measured annual precipitation (since 1931) and reconstructed precipitation at Crater Lake (from 1687 to 1930, based on the model derived through PCA) are shown in Fig. 3. The precipitation model based on tree growth represents interannual variation reasonably well, although several of the higher values are underestimated. Reconstructions often underestimate extreme values because tree-ring chronologies are based on a spatially variable aggregate of trees used to develop a time series of mean, rather than extreme, values (Fritts 1976, Fritts and Guiot 1990). High precipitation is indicated for the early and mid 1700s, the mid 1800s and the early 1900s. These general trends corroborate previous reconstructions of precipitation for the Pacific Northwest (Brubaker 1980, Graumlich 1987, Fritts 1991).

Measured lake level (since 1908) and reconstructed lake level at Crater Lake are shown in Fig. 4. Reconstructed lake level represents the general pattern of interannual variation in measurements reasonably well, although the magnitude of high and low extremes is underestimated. Mean reconstructed lake level during the measurement period (1908-1991: -92.2 cm) is less than that of the pre-measurement period (1687-1907: 175.7 cm). Mean reconstructed lake level during the 20th century (-84.8 cm) is much lower than that prior to 1850 (226.3 cm). Lake level starting in the late 1980s has been lower than at any time during the past 300 years except in the early 1930s to mid 1940s. Periods of greatest lake-level increases track periods of generally higher reconstructed precipitation (Brubaker 1980, Fritts 1991, Graumlich 1993) (Fig. 3).

Reconstructed lake level is generally much higher during the Little Ice Age than during the 20th century (Fig. 4). The highest reconstructed levels during the late 17th century are 9 m greater

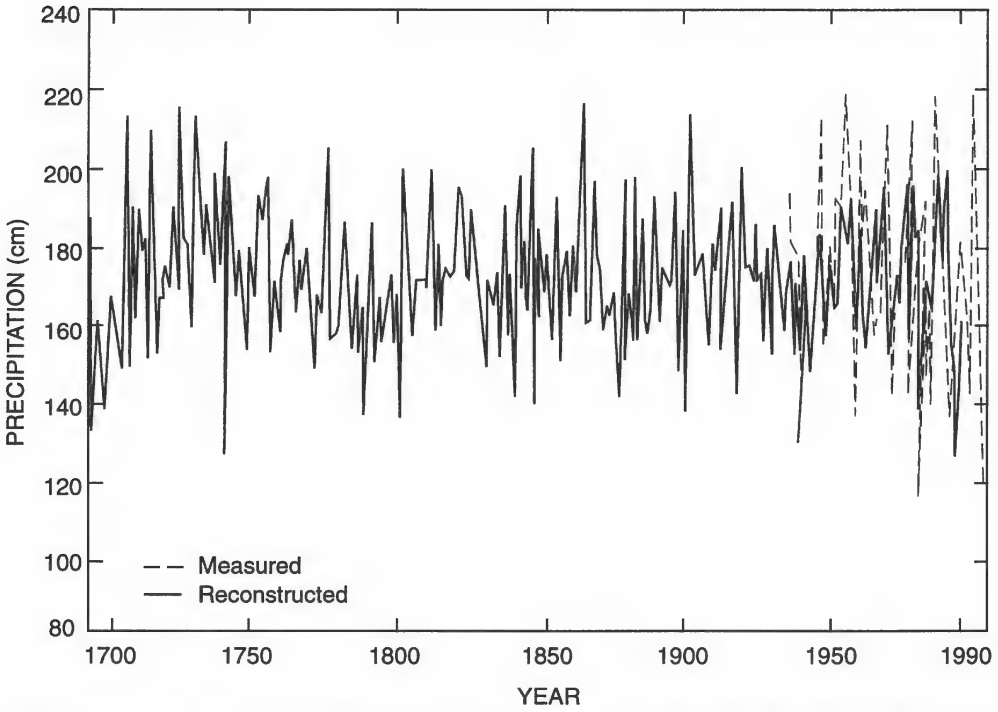

Figure 3. Measured (dashed line) and reconstructed (solid line) precipitation for the Crater Lake weather station, based on hydrological year (October through September). The reconstruction was extended to 1687, the point at which tree-growth data are available for a total of 25 trees and all 7 sampling sites are represented in the data set.

than the lowest measured levels of the 20th century. The magnitude of this lake-level change is supported by the fact that only younger trees (primarily *T. mertensiana* and *A. magnifica* <150 years old) are found along the lower wall of the caldera and shoreline of Wizard Island, compared to much older trees at higher elevations. The lowest lake levels (measured and reconstructed) occur during the early 1930s to mid 1940s, following a period of low precipitation in western North America (Graumlich 1993), including the Pacific Northwest (Graumlich 1987), with additional low levels starting in the late 1980s. The highest lake levels (reconstructed) occur in the mid 1700s, with evidence for additional high levels in the late 1600s. Even the lower peak in lake level in the mid 1800s is higher than any measured in the 20th century. If the model underpredicts extreme values as suggested by data for the 20th century, then the higher actual lake-level changes during the Little Ice Age may have been even higher than indicated by reconstructed values (Fig. 4); lower actual lake-level changes may have been lower than reconstructed as well.

Because the reconstructed parameter is lake-level *change* rather than *absolute* lake level (the sum of interannual changes, as shown in Fig. 4), it is difficult to directly link reconstructed precipitation (Fig. 3) and absolute lake level visually in the figures of reconstructed values. Another factor that obscures directionality of trends is that both standardization (a regression procedure) and regression modeling of the growth-index values produce time series with lower magnitude of variance than in the original data. Therefore, a small but persistent anomaly in precipitation—which would affect lake-level change—could be obscure in the reconstruction. Even if precipitation were relatively constant over time, but temperature was lower, as it surely was during the Little Ice Age, then lake level could have been higher prior to the 20th century as a

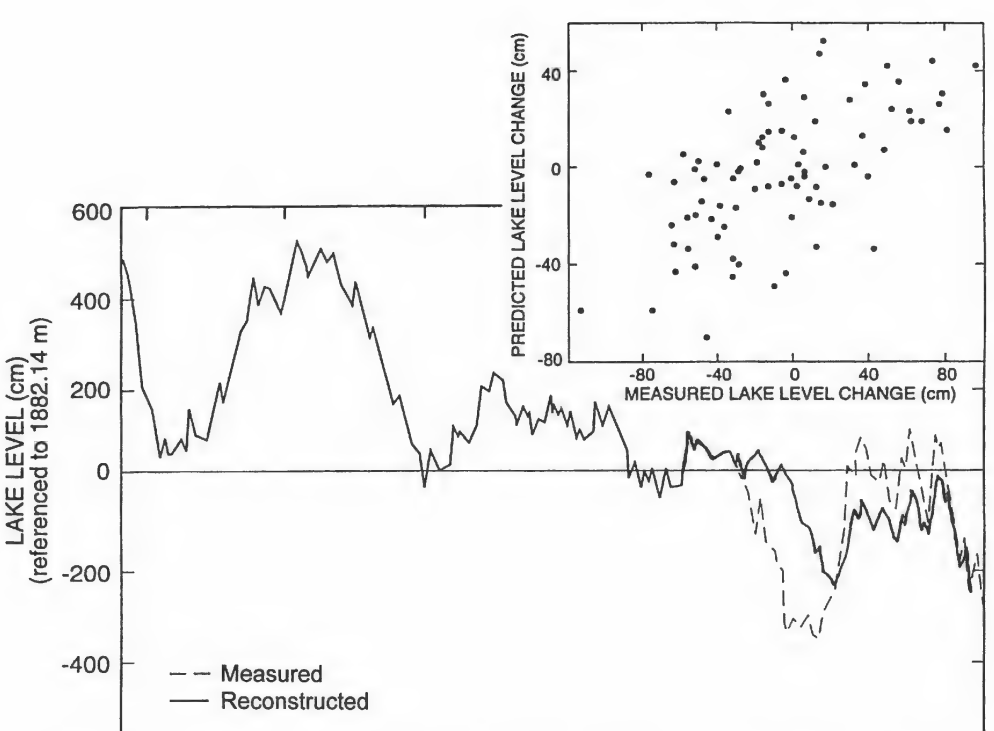

Figure 4. Measured (dashed line) and reconstructed (solid line) lake level for Crater Lake. Lake-level variations are adjusted to 30 September. Water stage is referenced to an elevation of 1,882.14 m above mean sea level and shown as a departure from this elevation (Redmond 1990). The reconstruction was extended to 1687, the point at which tree-growth data are available for a total of 25 trees and all 7 sampling sites are represented in the data set. The scatterplot shows the relationship between predicted and measured (since 1908) lake-level change (r^2=0.57).

result of lower evaporative rates. Lower temperatures could also have promoted ice formation on the lake, a very rare occurrence in the 20th century, thereby reducing winter evaporation.

Variation in atmospheric circulation can result in multidecadal anomalies of sufficient magnitude to produce significant changes in the water level of lakes and other bodies of water, as has been shown for California's Sierra Nevada (Stine 1990, 1994). The mid-latitude storm track of the northern hemisphere, which has a strong impact on general precipitation patterns in far western North America (Graumlich 1993, Stine 1994), may have tracked consistently over southern Oregon during the Little Ice Age. These conditions are supported by previous climatic reconstructions which indicate the prevalence of low pressure and high precipitation in this region during the latter half of the 17th century and much of the 18th century (Fritts 1991).

During the 20th century, periods of lower lake level coincide with the positive (dry, warm) phase of the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997), and periods of higher lake level coincide with the negative (wet, cool) phase of the PDO (Fig. 4). In addition, mountain hemlock chronologies from treeline at Crater Lake—and throughout most of the Pacific Northwest—are generally in phase with the PDO Index (PDOI) (Peterson and Peterson in review), and trees attain

more growth during periods with less snowpack (Smith and Laroque 1998). Conversely, low-elevation chronologies (especially in southern Oregon), for which high summer temperature can limit growth, are generally out of phase with the PDOI (Peterson and Peterson in review). These phenomena suggest that there are strong teleconnections among atmospheric circulation patterns, tree growth, and hydrology in southern Oregon. Because Crater Lake is so responsive to variation in precipitation, the PDO may have a significant influence on interdecadal variation in lake levels.

The climatically-sensitive hydrological system of Crater Lake, coupled with the dendrochronological record, is capable of tracking variation in regional precipitation. Even small changes in annual precipitation, including a few extreme years, can have a substantial cumulative impact on lake level. For example, the 9 m difference in lake level cited above can be accounted for by a deviation of only 3 cm/yr in precipitation (<2% of mean annual precipitation during the measurement period). Most assessments of the impact of climatic variability during the next century have focused on how potential *temperature* increases would affect natural resources (e.g., Watson et al. 1996). However, even small changes in *precipitation* can have major effects on hydrological systems (Arnell et al. 1996).

Lake-level variation and rates of lake-level change are straightforward hydrological effects of precipitation trends, and will reflect natural or human-induced variability in climate that may occur during the next century. Large, deep lakes are sensitive indicators of variation in precipitation if the lakes comprise a sufficiently large proportion of a watershed. Given the correlation between lake-level change and tree growth determined in this study, it may also be possible to use lake-level change as a means of estimating interannual and interdecadal tree growth. This would be a simple, economical approach for estimating temporal variability in forest productivity, which is an important indicator of ecosystem health. Crater Lake and other large lakes that dominate watershed surface area may be valuable for monitoring future changes in hydrology and productivity that result from variability in climatic patterns in the Pacific Northwest.

Acknowledgements

We appreciate review comments by Linda Brubaker, Robert Collier, Lisa Graumlich, Emily Heyerdahl, Gary Larson, Andrea Lloyd, Hugo Loaiciga, Steven McKay, Donald McKenzie, David Meko, David W. Peterson, Linda Wilkinson, Connie Woodhouse and Clinton Wright. Statistical review was provided by Loveday Conquest and Michael Arbaugh. Paige Eagle and Beth Rochefort assisted with figures. Research was supported by the Global Change Research Program of the U.S. Geological Survey, Biological Resources Division.

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Received January 31, 1999
Accepted for publication May 24, 1999

Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect) to the Editor.

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Politics, Book Reviews, Science, and White Lies: A Response to R. Gerald Wright

In his recent review of my book *White Goats, White Lies* (Lyman 1998), R. Gerald Wright (1998) does a reasonable job of restating the message I wished to convey. He is correct that I believe much of the "science" publicized by Olympic National Park regarding the "exotic" status of resident mountain goats (*Oreamnos americanus*) and their influence on local ecology lacks rigor and, it seems to me, objectivity. He is also correct that I do not "insist the park's conclusions are wrong" (Wright 1998:236). However, some statements he makes are misleading, and others misrepresent what I did and did not say. Lest Wright's statements become factoids, just as other statements have in the history of this particular wildlife-management controversy, I respond to several of them here.

Wright (1998:237) suggests that I perceive a "conspiracy" within the rank and file of Olympic National Park personnel to keep scientific truth—or at least scientific accuracy—from the published page. I never used the word "conspiracy" in *White Goats*. What I did do was document at length how only selected data and conclusions found in unpublished park reports were also found in the published record. Because I could not demonstrate that a conspiracy—what I take to be a conscious effort to mislead—was the cause of such selective publication, I suggested that white lies appeared in the published record because of sloppy science and an effort to maintain various factoids, particularly the often repeated one that *all* available evidence clearly and unambiguously indicated mountain goats are not native to Olympic National Park. It seemed to me that factoids—statements repeated so often that they become unquestioned dogma—resulted because what were perceived (consciously or not) by park personnel to be harmless errors of omission or commission were allowed to appear in the published record time and time again. A little digging through the literature suggested to me that white lies seemed to color every aspect of what is sometimes referred to as the Olympic National Park mountain-goat controversy (e.g., Scheffer 1993).

An example of Wright's belief that I perceive a conspiracy is the way he dispenses with various evidence I describe and discuss. For instance, he states that I "assume, with no substantiation, that changes in wording" of photograph captions "were part of the overall effort by park researchers to garner support for goat control" (Wright 1998:236). I "assumed" nothing, but rather attempted to determine and therefore *explain* why the wording of captions to historical photograph pairs changed between the early 1980s and the late 1980s. My explanation rested on two lines

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of evidence: the nature of the wording changes and the different contexts in which the captions are found. The wording changed from "perhaps," "probably," and "park researchers believe" mountain goats were responsible, to goats "were" the miscreants responsible for the differences in the photographs. Simultaneous with this change in wording, the context shifted from limited distribution reports with "not for publication" on their covers to published and widely circulated articles and monographs. I did not ask the park why the wording changed; they had stopped communicating with me when I was writing the book because I was asking them just such questions (Lyman 1998:216). If Wright or park researchers have a different explanation, I would like to hear it.

The statement by Wright (1998:237) that I criticize Susan Schultz's summary of nineteenth and early twentieth century documents regarding the presence or absence of mountain goats in the Olympic Mountains in part because she "purposely omitted" "historic accounts which report mountain goats in the Olympics" is simply false. I said "apparently, Schultz did not discover" a historical report of mountain goats in the Olympics (Lyman 1998:124). I said "apparently" because when I pointed out this oversight in the pages of this journal (Lyman 1995), park biologist Doug Houston (1995:239) responded that Schultz had "simply overlooked it." But park researchers had admitted to previously "purposely" omitting reference to reports that contradicted their favored viewpoint (Wagner et al. 1995:105), a point I made in the book (Lyman 1998:117–118). I therefore could not trust Houston's explanation, but rather than say Schultz "purposely" omitted a potentially key bit of information, I said she had apparently not discovered it.

It is potentially misleading on two counts for Wright to state that I have "support from animal rights advocates and portions of the general public." First, this statement could be taken to signify that I received financial support from either or both of the two named factions. I have never received any such support from any individual or faction. I acknowledged in *White Goats* that Fund for Animals personnel sent me copies of park reports and various correspondence they had found in park offices or had received from Olympic National Park; they also kept me apprised of what was happening 3,000 kilometers away from my office. Second, I noted in the book (Lyman 1998:vii) that I disagree with Fund for Animals personnel on certain conclusions and implications of various data. The latter is not mentioned by Wright, and thus his omission might be taken to signify that I and those who "support" me agree on all counts. We do not.

Wright (1998:237) states that I offer "little support for statements like [reviewers of the park's reports]... 'did not evaluate that evidence in any manner, nor did they have all the evidence at their disposal'" (Lyman 1998:218). This statement concerns a 1993 review by nine people of four documents, particularly the document on archaeological data. I devoted 10 pages (Lyman 1998:138–147) to supporting this statement specifically. I spoke with one of the nine individuals and s/he had no idea there was much more "evidence" of which the park had not made the reviewers aware. Wright does not mention that I applauded when some reviewers included evidence that had not been considered in "the park's reports" in their reviews. It was at first unclear to me how Wright could suggest I make unsupported statements when it is documented in *White Goats* that what the nine reviewers received was secondary information in the form of synoptic summary documents rather than primary evidence in the form of the original reports of late nineteenth- and early twentieth-century authors. After some thought, I suspect Wright is parroting the park response to precisely this same critique of this particular review made by myself and others. Park personnel did not agree with the significance of this critique; apparently, neither does Wright.

Saying that Wright is parroting park responses to my efforts also characterizes his suggestion that I do not introduce "much new evidence" (Wright 1998:236), a comment I have also received from the park. In some cases the comment is true, in other cases it is not. With respect to the latter, and taking "new" to signify evidence not considered by the park in their reports, I introduce "new" local archaeological data that increases the park's evidence by over 40% (Lyman 1998:141). I introduce "new" turn-of-the-century documents on the distribution of mountain goats (pp. 120–122). I did not do a new field survey of the goat population, but I introduce a "new" estimate of the population size that I thought was more statistically valid (pp. 48–50). I introduce "new" historical

documents that concern why goats were introduced to what were a few years later to become park lands (p. 105). And I introduce "new" zoogeographic and phytogeographic evidence (pp. 157–162, 172–184). Park researchers had, as I admitted, already introduced much of the relevant evidence. My points were that what they had introduced was selective and biased, and that their repeated contention that *all relevant evidence* had been introduced could not be maintained.

Wright (1998:236) suggests that I "seem to lack an appreciation of the difficulties of counting animals in such an environment or the fact that this was the first detailed census of mountain goats in the park and was thus a learning experience." I explicitly outline in the book some of the requisite assumptions and problems with population-estimation techniques in general (Lyman 1998:37–38), and although I do not indicate the 1983 census was "the first detailed census," I do point out that the several population estimates rendered before that census were found unacceptable by park biologists and that they wanted a more rigorous estimate (pp. 38–41). Much of the chapter on population size documents in detail the difficulties that have plagued the park's efforts to obtain a population estimate plus the fact that park biologists have treated those estimates as interval-scale measures. That chapter also documents that park biologists accept and publicize estimates that the park's mountain-goat population is large, and discount and do not publicize estimates suggesting the population is small. For example, Wright, subsequent to that first "detailed census," made an "educated guess" regarding the size of Olympic National Park's mountain-goat population in an unpublished report. That guess is larger than any other estimate mentioned anywhere. As I note in the book (pp. 62–63), Wright's guess also appears in the widely-circulated and park-authored 1995 Draft EIS on park mountain goats. I suggest it appears there, because, as Wright (1998:236) notes, "the numbers of mountain goats in the park are important in making a case for the urgency of control." Larger numbers signify greater urgency.

Perhaps the most misunderstood argument I present in *White Goats* and elsewhere is my suggestion that archaeological and paleontological research be used to help establish the presence or absence of taxa in an area where historical records are lacking, ambiguous, or contradictory. Wright (1998:237) displays his version of this misunderstanding when he states that "following this logic to the extreme would make it virtually impossible for the NPS to conclude any species was non-native." I have never suggested that it should be followed to any extreme (e.g., Lyman 1988, 1994). As I noted in the book (Lyman 1998:221), to do so would be to fall prey to what biologist Michael Hutchins (1995) refers to as the "paralysis of analysis," an option park personnel and I agree is unacceptable. Therefore, I tried to establish an amount of archaeological work that would allow us to reasonably conclude that the absence of mountain-goat remains implied an absence of goats prior to 1925 (Lyman 1998:142–143). My logic was simple and can be illustrated with an example. If a researcher does not read *Northwest Science*, s/he will not find Wright's review of *White Goats*. Park researchers had not, in my view, examined any issue of *Northwest Science*, and I suggested how many issues they should read before concluding Wright's review did not exist.

In the last paragraph of his review, Wright indicates that the substance of *White Goats* "may be a moot point," as "social and political criteria" may be the ultimate arbiter in the controversy. Olympic National Park has always argued that the decision should be based on science, and science was the focus of my book. It would be a shame, let alone a travesty, were Wright's prediction to come true. That is in part why I called for a thorough review of *all* pertinent evidence, an action that, I indicated in the book, the park is attempting to implement.

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What's the Dam Problem? Breaching Four on the Lower Snake River

Salmonid stocks in the Snake River Basin have declined steadily since the completion of four federal dams between 1962 and 1975: Ice Harbor, Lower Monumental, Little Goose, and Lower Granite. The "four H's"—hydroelectric, habitat, hatchery, and harvest—have been identified as the culprits responsible for salmon decline. Combined impacts from the four H's are devastating. On the Snake River, coho salmon are extinct, sockeye salmon are listed as endangered, and spring, summer, and fall chinook are listed as threatened (Wik 1995). These dams are directly related to the high salmon mortality rate in the Snake River (Yates and Curtis 1998).

Dams such as Chief Joseph on the Columbia River and Hells Canyon on the Snake River have no adult fish passage facilities. The lack of fish ladders eliminated spawning habitat upstream of these dams (Wik 1995). However, the dam passage issue is more serious in terms of juvenile downstream migration. Dams that lack juvenile fish passage facilities such as turbine screens and bypass channels experience severe smolt mortality. It is estimated that between 7 and 32 percent of smolts die at each dam (Muckleston 1990). "Turbines do not puree these small salmon, rather they kill by creating violent pressure changes that can explode a salmon's swim bladder" (Harden 1996). The juvenile fish that survive the dam bypass system are still at great risk. Those that are not killed are usually stunned and sluggish, making them easy targets for seagulls and other piscivorous fish. Federal agencies have concentrated their efforts on transporting juvenile fish "out of river". Migrating juvenile fish are collected and put on barges or trucks and transported downstream of the last federal dam on the Columbia River, Bonneville Dam. This unnatural practice has been the U.S. Army Corps of Engineers' method of salmon restoration for the past twenty years, and it has come under severe fire from scientists and environmentalists. Distilling juvenile salmon from the river and transporting them in mass quantities cause environmental stress. The stress makes the fish more susceptible to disease and predators upon release below Bonneville. Furthermore, transporting salmonids out of river interferes with the imprinting process that allows them to return to their natal streams (Harden 1996). There is data to support the fact that barging has yielded zero improvement on returning stocks, yet it remains a popular "mitigation" method.

Juvenile fish that remain in the river to migrate to the sea encounter more perils. The dams have created stagnant reservoirs of water, thus making the downstream journey more difficult. The low velocity of the pools causes delays in migration, requiring two to three months in slackwater compared to less than one month before dams were constructed. Temperature of reservoir water is much higher than that of free flowing water. Salmonids have a low tolerance for warm water with about 70°F being the upper lethal limit; temperatures in excess of 74°F were recorded on the Snake River during the summer of 1998 (Barcott 1999). These deep, warm water reservoirs also provide excellent habitat for non-native predators of juvenile salmon, such as smallmouth bass. Warm temperatures impair the immune system of the fish and lead to increased disease.

The incredible loss of salmon in the Snake and Columbia River Basins has prompted the federal government to act, after seeing two decades of smolt transportation fail to reverse the decline in fish stocks. A restoration plan developed by the National Marine Fisheries Service (NMFS) cites two possible courses of action. The first is to continue transporting fish with fish passage improvements and increased flow augmentation. Flow augmentation refers to the releasing of extra water (in this scenario, up to one million acre-feet) stored in Snake River Basin reservoirs to aid fish migration. The second approach is breaching the four lower Snake River dams and permanently drawing down the reservoir behind John Day Dam on the mainstem of the Columbia (Blumm et al. 1998). There is considerable support

and opposition to both of these scenarios, but science and economics dictate that the latter is the only way to save Snake River salmon.

Improving fish passage structures at many dams will allow safer in-stream migration for juvenile salmon. The additional flow augmentation will also speed up downstream migration. However, transporting fish has not proven successful over the past two decades, and there is no reason to believe that the program will ameliorate current declining conditions. The emerging consensus in the scientific community states that returning the river to "normative" conditions is the best way to recover Snake River salmon. Breaching the four lower Snake River dams would remove passage barriers, restore a more natural flow regime to aid both upstream and downstream migration, and create shoreline habitat for juvenile rearing and feeding. In fact, the Idaho Department of Fish and Game stated in May 1998 that breaching the dams and restoring natural river conditions "is the best biological choice for recovering salmon and steelhead in Idaho" (Yates and Curtis 1998). Breaching may be a misleading term for what the Army Corps of Engineers proposes to do. In fact, dam breaching is more akin to dam bypassing. A new bypass structure would be created on one side of the dam through the removal of existing earth-fill dam sections or bedrock. A new river channel would be dredged through the bypass, and flow would be diverted around the existing powerhouse. The cost of dam bypassing for all four dams is near $5 billion and does not include mitigation, impacts to navigation and agriculture, or loss of power generation (Wik 1995).

Nonetheless, dam breaching proponents argue that the Northwest can do without the four dams on the lower Snake River. In terms of regional electricity generation, they produce only 4 percent of the total power. The permanent drawdown of John Day reservoir would amount to another 7 percent loss in power generation (Yates and Curtis 1998). The dams do not serve any flood control purpose. Three of the four lower Snake River dams do not provide agricultural irrigation; Lower Granite does provide irrigation for a golf course. Ice Harbor Dam is the only irrigation dam, and it provides water for all 13 farmers in the region (Barcott 1999). Therefore, the economic burden on the region does not outweigh the burden of salmon extinction.

There are major losers in the dam breaching scenario. The ports of Lewiston, Idaho and Clarkston, Washington would become landlocked once again. Free flowing water on the Snake River would essentially shut down the barging industry. Currently, agricultural products from Oregon, Washington and Idaho are efficiently and cheaply shipped to Portland from Lewiston and Clarkston. New methods of transporting these goods would be needed, most likely in the form of rail or truck (Yates and Curtis 1998). Goods would need to be transported to the nearest barge port on the Columbia, and barge transportation would be eliminated on the Snake. The reservoir habitat created by pooling of water behind the dams would be eliminated. Resident fish populations would be greatly affected if the river were to return to a free flowing state. In 1992, the Army Corps of Engineers executed a test drawdown of Lower Granite and Little Goose Dams. The results of the test were not very encouraging. Sediments became resuspended in the water after accumulating behind the dams. Major losses of resident fish and benthic organisms were observed (Wik 1995). The test drawdown should not be viewed as equivalent to dam breaching since two dams still existed below the test dams, and the effects of bypassing all four dams are still being researched.

People live in the Northwest for its excellent quality of life. Salmon are a part of the region's culture, as well as the ecosystem. To lose such an icon would be devastating to the quality of life in the Northwest. The Army Corps of Engineers was to have its report on dam breaching prepared by April 1999. The Corps managed to have the deadline on the report pushed back to December 1999. In the meantime, different interest groups with a stake in Snake River dams and salmon will continue the breaching debate. It is unlikely that a consensus will be reached among the various river interests. However, every citizen of the Northwest must think hard about what extinction of Snake River salmon means to them. As the old cliché goes, extinction is forever.

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Book Reviews

Yellowstone and the Biology of Time: Photographs across a Century

Mary Meagher and Douglas B. Houston, 1998, University of Oklahoma Press (Cloth $80.00, ISBN 0-8061-2996-4; paper $32.95, ISBN 0-8061-3006-7).

"I wish I could have seen this place a hundred years ago." Nearly all of us have uttered that phrase at one time or another, and thanks to a creative photo-filled book, we can now take that step back in time for Yellowstone National Park. *Yellowstone and the Biology of Time* is a landmark volume in the retrospective analysis of parks and protected areas. This chronology of landscape change trumpets the message that ecosystems are dynamic over a wide range of spatial and temporal scales.

Forest Service scientist George Gruell pioneered the use of repeat photography to document ecological change in his classic studies of Montana and Wyoming landscapes published in the early 1980s. Biogeographer Thomas Veblen also used this technique in an interesting analysis of the Colorado Front Range published in 1991. Biologists Mary Meagher and Douglas Houston, both retired federal scientists who spent most of their careers with the National Park Service, follow in this tradition with a heroic effort of repeat photography that provides good spatial coverage of Yellowstone over 120 years.

As Meagher and Houston tell us in the preface, the book had a gestation period of 25 years. They first compiled an impressive collection of photos from the Yellowstone archives, most of which were taken by W. H. Jackson, J. P. Iddings, F. J. Haynes, and J. E. Haynes during the late 1800s. Between 1971 and 1973, they relocated the scenes in the old photos and compiled a new set of photos. A number of logistic difficulties kept them from completing the project, then the fires of 1988 occurred, providing an opportunity to document the effects of large-scale disturbance. So they took another set of photographs. We were fortunate that the authors delayed the publication long enough to capture this critical milestone in ecological time!

The historical photos in *Yellowstone and the Biology of Time* are striking in their beauty and clarity. The cumbersome technology of a century ago must have posed considerable challenge for photographers working in the outdoors, particularly in the backcountry. It is therefore not surprising that many of the photos are adjacent to roads. But that also affords us the opportunity to see the effects of human activities, both historical and contemporary. It is heartening to see the restoration of many sites that were previously heavily grazed by cattle, cut for hay, and used for Army encampments. Conversely we can also see the degradation of modern-day sites by buildings and parking lots.

Brief, descriptive text interprets each photo set with ecological, historical, and context; on-ground examination of each site by the authors provides helpful information on plant species and other characteristics not apparent to the casual observer. The photos point out dramatic changes in many geothermal features. They also indicate that many of the aquatic systems are surprisingly dynamic in terms of extent, water level, and associated vegetation. Beavers, whose near-elimination has altered the aquatic ecology of Yellowstone, apparently act as a keystone species and may deserve more study with regard to effects that cascade to other species.

The photos also demonstrate that the magnitude of changes in vegetation are extraordinarily site-specific in Yellowstone. Change appears to be relatively fast at many low-elevation sites, but considerably slower at higher elevations (in the absence of fire). Variation in the distribution and abundance of big sagebrush over time is a striking feature in many photos. Reduced cover of quaking aspen and willows, which is cited by some as evidence of "overgrazing" by native ungulates, is apparent in many photos. However, there are also photos that indicate an increase in these species at some locations in the park. The post-fire photos show a mosaic of effects to forest overstory and shrub-steppe species.

Photos give way to summaries of the physical and biological framework of Yellowstone, including geology, climate, soil, and vegetation, as well as discussion of the interaction of climate, fire,

grazing, and human activities on the dynamics of present-day ecosystems. These sections are rather brief, but they cover the basics. Some readers will be disappointed that the authors do not include detailed discussion of the seemingly endless debates about management of the charismatic megafauna of Yellowstone. Indeed, Meagher and Houston were embroiled in these debates for many years. To their credit, the authors discuss wildlife management and alternative viewpoints evenhandedly from a *scientific* perspective. Proponents on any side of current issues related to elk and bison management will not find much fodder for advocacy positions here.

The book has few shortcomings. It would have been nice to see greater consideration of ecosystem dynamics outside the boundary of Yellowstone National Park, particularly given the long-standing existence of interagency assessments and management activities within the Greater Yellowstone region. Appendix 2 summarizes temporal changes by vegetation type as seen in photos, but it is not particularly useful due to the high variability between sites. I was also hoping for some better maps, given the ready availability of GIS coverages for Yellowstone.

Yellowstone and the Biology of Time is intended for a general audience. It provides a solid background on basic ecology, natural history, and landscape dynamics for the layperson, and includes sufficient information to hold the interest of those with some technical training in biology. Scientists may be disappointed that the book simply summarizes resource management issues and scientific controversies, rather than shedding much new light on them. The most frequent users of the book will likely be Yellowstone afficionados—those who work in the park, visit it frequently, or otherwise have a strong connection to the park's resources. Fortunately the moderately-priced paperbound version will make the book accessible to many readers.

I hope that some enterprising individual will now develop a Web-based archive to provide broader access to this important collection of photos. By having digital images catalogued by topic and geographic location, future photographers—or landscape detectives, as Meagher and Houston call them—will be able to locate particular scenes and add new photos to the archive. All parks and protected areas should consider developing this type of electronic archive, which would be a dynamic information source for scientists, resource managers, and the general public.

If you are planning a trip to Yellowstone, buy a copy of *Yellowstone and the Biology of Time*. Read it before you go, then take it with you and note the photo points along the roads and trails. As a modern-day time traveler, you will be able to more fully experience the dynamic Yellowstone landscape.

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Mammals of the Pacific Northwest: From the Coast to the High Cascades

Chris Maser, 1998, Oregon State University Press ($26.95)

Mammals of the Pacific Northwest is as much a personal journey as it is a natural history of mammals of the region. Most vertebrate ecologists of Maser's generation grew up as kids fascinated by the animals around them; they crawled through bushes, waded in marshes, and caught everything that came within reach. Few have remained naturalists because science, even vertebrate science, has rapidly moved in the direction of rigorous hypothesis testing, experimental design, and high powered statistical analysis. There seems to be little place for naturalists in this new climate, and that is our loss.

Few people, scientists or otherwise, have had as extensive and intensive studies and personal interactions with as many mammalian species as Maser. For that reason alone, the book is a treasure trove of fact, observation, and supposition, from the diets of bats to observations of personality differences among individual shrews. In this book Maser presents a lifetime of observations from a distance to up-close and personal. As Maser himself says in the introduction: "I have now spent over thirty years in a consummate love affair with science—mostly studying mammals in the wild . . ."; "I have over many years learned to know them." Indeed he has.

Mammals of the Pacific Northwest is not a field guide, and it doesn't pretend to be one, although most of the information found in field guides is present in this book as well. It is a taxonomically arranged natural history of these animals, interspersed with some delightfully poignant and occasionally hilarious remembrances of particular individual mammals or events, and as such is remarkably readable. Because it is written from the naturalist's perspective, this is the book that the serious student of mammals should read before going out in the field to observe, trap, or study mammals. To borrow from current vernacular, this book helps one to "get inside" an animal's head, an ability often lacking in current generations that haven't had the luxury of many years of patient first-hand observation.

Maser has organized the book in about the only sensible way it could be, in standard taxonomic fashion beginning with the most primitive and culminating with the most advanced. Although not a critical fault, it is unfortunate that when it comes to taxonomy, Maser adheres to his past. He retains the taxonomy he learned as a student and with which he is comfortable, regardless of whether it is correct. For example, the Townsend Chipmunk was revised into (in Oregon) 3 species in 1974; 25 years should be a sufficiently long time to warrant more than an acknowledgment that "Some authorities now separate the Townsend Chipmunk into three species, *T. townsendi, T. senex, and T. siskiyou"* (page 133).

In similar fashion Maser has retained his familiar English-system measurements in the species descriptions, although in fairness, metric equivalents have been added into the margins. I personally find it cumbersome to have to read: (for example: Botta pocket gopher, page 179) "They are 7 5/8 to 10 7/8 inches with tails that vary from 2 1/4 to 3 7/8 inches in length." Even for someone refusing to relinquish their familiar English measurements, 7.5 to 11 inches would have been sufficient.

Maser would also have been well-advised to omit his attempt at explaining evolution, speciation, and the diversity-stability question. It adds little to the book; on the contrary it begs correction or, at least, further clarification. Fortunately the book is intended for a general audience and these passages will not be critical to the overall evaluation or enjoyment of it. Nevertheless, I wish these explanations had never been attempted at all, rather than the simplistic and muddled discussion that is presented.

Maser's objective was to reach a general audience, and to share his life-long love affair with Pacific Northwest mammals both by presenting his vast storehouse of life history knowledge and by telling interesting (if not endearing) stories of individual animals he has known. I think he has succeeded. Readers will get an enhanced view of what otherwise would be a series of entries in

a field guide; I believe this was Maser's intent. As a professional ecologist, this would be the first source I would want to read if I wanted to learn more about a mammal I planned to study.

—Bruce E. Coblentz
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Oregon's Living Landscapes—Strategies and Opportunities to Conserve Biodiversity

Oregon Biodiversity Project, 1998, Defenders of Wildlife ($29.95)

The Oregon Biodiversity Project has compiled and interpreted biological facts, figures and information from over 50 partners into beautiful and informative "big picture" view of the state of Oregon's biodiversity. With impressive photographs, powerful maps and level headed prose, the Oregon Biodiversity Project successfully informs the reader about the immense biological diversity, resource management issues, and responsibilities such diversity demands. The authors never attempt to satisfy all stakeholders managing Oregon's diversity. But the book itself is an encouraging step toward increased cooperation, even among historically opposite interests. Throughout, the book remains true to its title. It describes the biological diversity and continually provides common sense visions and strategies for its preservation.

This strategy guidebook begins with a good working definition section clearly defining biodiversity and its importance, a major theme of the book. The definitions provide the reader with the perspectives of the authors. This allows one to view the issues from a cooperative, no-fault perspective.

A short section addresses the loss of biodiversity. Instead of placing blame, the book places the loss of biodiversity into broad categories including habitat destruction, fragmentation, degradation, introduction of non-native species, and exploitation and overharvesting of resources. Each threat to biodiversity is defined and discussed. Discussions of scale, species richness and classifications follow, staying true to a theme of simplicity coupled with good science and a cooperative spirit.

The next chapter provides the reader with a state-wide strategy for conserving biodiversity. Several broad agency and stakeholder suggestions are made with intent to promote a sense of community and mutual interest, and to foster respect among people with differing perspectives. The difficulty of such an initiative is never trivialized, but cooperation must continue and expand if the goal of conservation is to be achieved. The chapter ends by restating common themes found throughout the book: ecosystems are dynamic and conservation is a process, not a product.

A real strength of the book is first demonstrated in the third chapter. Here, the framework for a statewide overview of Oregon's biodiversity is laid out with detailed color maps. These maps were compiled mostly from the Oregon Gap Analysis Project, which sought to identify knowledge gaps in biodiversity protection. They begin to provide a "coarse filter" look at a large number of different topics ranging from the percentage of public land ownership, to core areas for salmon and steelhead. These maps are common through the remainder of the book. They provide great detail for regional trends, and showcase the flexibility and power of current GIS techniques. The maps could stand alone to prove their intended points, but they are always wrapped in plain language explanations. The resolution of the maps is sometimes poor, but this is always explained and conceded by the authors. It seems as if earning the readers trust by providing unbiased information is as important as presenting the data.

Chapter four is devoted to an in depth look at Oregon's 10 ecoregions. An ecoregion approach was chosen over a watershed approach because the ecoregion boundaries are based on physical features and conditions which often combine very different ecosystems. Each has its own vegetation and aquatic species analysis, a summary of conservation issues and partners and, finally, a section suggesting conservation opportunities at the landscape level. This chapter is by far the longest in the book, and is packed with information. The information is consistently referenced and supported by a fair-sized bibliography of state, federal and commercial studies. Each section highlights a dominant feature or concern, and provides surprising detail for all areas, large and small.

The book ends with a short conclusion which attempts to reiterate major biodiversity themes and concerns by suggesting both esoteric and concrete ideas for continuing or improved conservation of biodiversity. The conclusion also provides policy and management suggestions for using the political systems in place in Oregon, and applying common sense to improve a good, but not great, conservation system. A final few

paragraphs offer suggestions for Oregonians regardless of where they might live or their chosen vocation.

Oregon's Living Landscape—Strategies and Opportunities to Conserve Biodiversity is both the title and best descriptive phrase to use for this colorful, clear headed collaboration from the Defenders of Wildlife, The Nature Conservancy, the Oregon Biodiversity Project and numerous other partners. As a reference book or a primer for Oregon and biodiversity, this book is informative, useful and fun.

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NORTHWEST SCIENCE

Information for Authors

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- Text (Introduction through Acknowledgments)
- Literature Cited
- Footnotes
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Monographs or books

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Theses, dissertations, personal communications, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary pons in Alberta. University of Calgary, Calgary. M.S. Thesis.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. University of Utah, Salt Lake City. Ph.D. Dissertation.

Danwiddie, P. W. In Press. Dichotomous key to conifer foliage in the Pacific Northwest. Northwest Science.

Technical Bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agricultural Experiment Station Technical Bulletin 60. Washington State University. 210 p.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA Forest Service Research Paper RM-214. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. 39 p.

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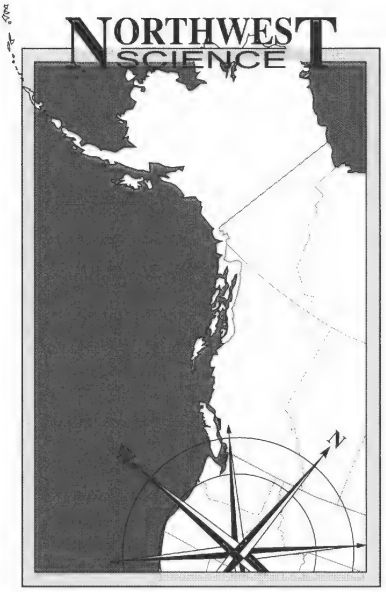

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Quarterly Publication of the Northwest Scientific Association

Nonprofit Organization
U.S. Postage
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Pullman, WA
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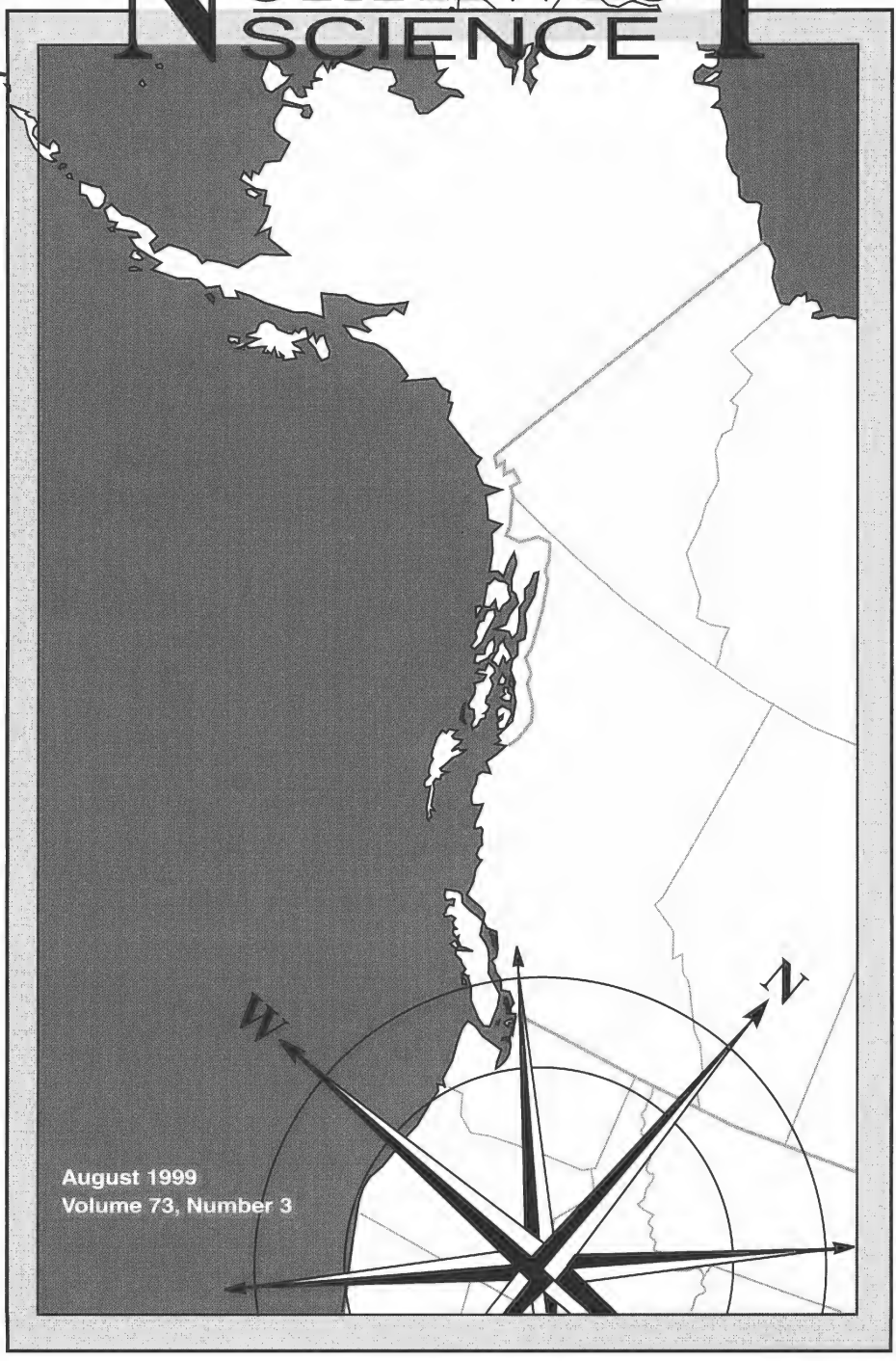

August 1999
Volume 73, Number 3

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Announcements

Annual Meeting, University of Idaho, March 16-19, 2000

The 73rd annual meeting of the Northwest Scientific Association will be hosted by the University of Idaho at its campus in Moscow, Idaho, on March 16-19, 2000. Following a business meeting of the governing board on March 16, scientific sessions will occur on the following two days with a variety of concurrent sessions and symposia.

Members and nonmembers are welcome at the meetings, and students are especially encouraged to attend and report the results of their research at the meeting.

A final, more detailed announcement will be in the November issue of *Northwest Science,* and a call for abstracts and meeting registration information will be mailed to all members.

R. K. Tveten and **R. W. Fonda**[1], Department of Biology, Western Washington University, Bellingham, Washington, 98225

Fire Effects on Prairies and Oak Woodlands on Fort Lewis, Washington

Abstract

Before 1800, frequent fires maintained Idaho fescue prairies and Garry oak woodlands on Fort Lewis. Fire exclusion in the 1900s, however, has allowed Scot's broom, Douglas-fir, and numerous herbaceous aliens to invade native prairies and oak woodlands. Since 1978, a management program using prescribed fires on 3-5 yr rotations has been used in an effort to maintain the open communities. We evaluated the role of fire on fescue prairies, oak woodlands, and broom thickets using prescribed fires in fall 1994 and spring 1995, and compared preburn/postburn species frequency to identify fire maintainers, increasers, and decreasers. Fall fires were more effective than spring fires, and best promoted native species and communities. Prescribed fires had no effect on Idaho fescue frequency, which maintained dominance in the postfire prairie. Other native prairie graminoids and forbs, and hairy cats-ear, a prominent alien, were maintained by fire. Prescribed fires also maintained open Garry oak woodlands, reduced Scot's broom cover in broom thickets, and killed small Douglas-firs. These fires, however, tended to favor alien species instead of native species. A large prairie subjected to >50 yr of broadcast burns ignited annually by artillery fire has been converted from fescue prairie to an open meadow dominated by hairy cats-ear and alien grasses, such as sweet vernal grass. Of the three regimes we investigated, fire intervals shorter or longer than the 3-5 yr fire rotation now employed on Fort Lewis are detrimental to fescue prairie and oak woodland. Excessive burning or fire exclusion causes loss of prairie and oak woodland.

Introduction

In regions where recurring fire is an important environmental factor, many plant species have fire-tolerant characteristics and persist despite repeated fires. Some plant communities are fire-dependent, persisting only where fires prevent more competitive, fire-sensitive species from displacing them. Fire-stable communities are maintained by frequent, low intensity, low severity ground fires that exclude invasive, fire-avoiding species (Anderson and Brown 1986, Agee 1993, Fonda et al. 1998). Fire-stable communities include prairies (Kucera and Ehrenreich 1962, Anderson 1964, Ewing and Engle 1988, Wilson and Shay 1990), oak woodlands (Plumb and McDonald 1981, White 1983, Guerin 1993), chaparral (Horton and Krabel 1955, Vogl and Shorr 1972, Conrad et al. 1986), ponderosa pine (*Pinus ponderosa*) forests (Weaver 1964, Covington et al. 1997), and longleaf pine (*P. palustris*) forests (Greene 1931, Rebertus et al. 1989).

Most native prairie species endure fire extremely well (Anderson 1964, Old 1969, Heady 1972, Antos et al. 1986, Ewing and Engle 1988, Wilson and Shay 1990). Fires maintain prairies by killing invading trees and shrubs (Thilenius 1964, Griffin 1977, Nimir and Payne 1978, Gruell et al. 1986). Both Nimir and Payne (1978) and Antos et al. (1986) quantified the effects of fires on Montana prairies with species composition similar to prairies on Fort Lewis, Washington, the location of this study. Prescribed fires set in spring by Nimir and Payne (1978) initially changed the cover of some prairie species, but those differences decreased throughout the first growing season. Antos et al. (1986) observed that a summer wildfire initially reduced Idaho fescue (*Festuca idahoensis*) cover and increased total forb cover, although the community returned to preburn cover values within three years. Neither of these studies provided data on species frequency, however, which would have clarified to what extent the species endured fire.

The effects of fire on communities dominated by oaks have been studied extensively (Boerner 1981, White 1983, Myers 1985, Guerin 1993, Glitzenstein et al. 1995), especially in California (Heady 1972, Green 1979, Plumb and McDonald 1981, Sugihara and Reed 1987, Allen-Diaz and Bartolome 1992). Some oaks are fire resisters (Rowe 1983), protected from fire damage by thick bark (Plumb 1979), but more commonly they are fire endurers (Rowe 1983), relying on postfire resprouting after top-kill (Boerner 1981, Plumb and McDonald 1981, White 1983, Myers 1985, Allen-Diaz and Bartolome 1992, Keeley 1992, Guerin 1993). Prescribed fires maintain open Garry

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oak (*Quercus garryana*) woodlands by reducing shrub cover, killing invading conifers, and top-killing oak sprouts (Plumb and McDonald 1981, White 1983). Sugihara and Reed (1987) set fall fires in California to maintain Garry oak woodlands. Fires killed Douglas-fir (*Pseudotsuga menziesii*), but mature Garry oaks were not damaged. Fires top-killed all oak stems <3 m tall, but all damaged stems resprouted vigorously.

Since the late 1800s, fire exclusion has reduced fire incidence in many fire-stable communities, so that fire-dependent plant communities have been invaded by fire-sensitive species (Cooper 1961, Weaver 1964, Myers 1985, Agee 1993). Fire exclusion also permits high fuel levels to develop, which ultimately may lead to high intensity, high severity fires that threaten normally fire tolerant communities (Gartner and Thompson 1972, Habeck and Mutch 1973, Griffin 1977, Gruell et al. 1982).

Prescribed fires, similar to those we used in this research, are designed to reduce fuels, remove invasive species, and maintain fire-dependent communities. Prescribed fires commonly are set in prairies (Heady 1972, 1977; Nimir and Payne 1978; Anderson and Brown 1986; Gruell et al. 1986), oak woodlands (Sugihara and Reed 1987), ponderosa pine forests (Weaver 1964, Ffolliott and Guertin 1988), longleaf pine forests (Guerin 1993), and giant sequoia (*Sequoiadendron giganteum*) forests (Kilgore 1972, Parsons and Nichols 1985).

Douglas-fir is a commonly targeted species of prescribed fire, because Douglas-fir benefits from fire exclusion on prairies and open woodlands throughout its range. Since the advent of fire exclusion, Douglas-fir has invaded prairies in Montana and Washington (Cooper 1961, del Moral and Deardorff 1976, Agee and Dunwiddie 1984, Gruell et al. 1986), and oak woodlands in Washington, Oregon, and California (Sprague and Hansen 1946, Lang 1961, Thilenius 1964, Franklin and Dyrness 1973, Kertis 1986, Sugihara and Reed 1987). The effectiveness of prescribed fire at removing invading Douglas-fir from prairies and oak woodlands has been studied in Montana (Gruell et al. 1986) and California (Sugihara and Reed 1987), but not in western Washington. Gruell et al. (1986) noted that spring and fall fires caused high mortality among small Douglas-firs. Fall fires burned more thoroughly, and they tended to kill larger trees. Sugihara and Reed (1987) concluded that fall burning every 5 yr, coupled with mechanical removal of occasional Douglas-fir survivors, maintained Garry oak woodlands.

The study site for this research was Fort Lewis, a 34,865 ha military installation ~20 km south of Tacoma, Washington. Idaho fescue prairies, Garry oak woodlands, and Douglas-fir forests are dominant community types on Fort Lewis (Figure 1). The prairies and oak woodlands of Fort Lewis exist on gravelly, glacial outwash plains deposited ~14,000 yr ago (Ugolini and Schlichte 1973). The soils are classified as Spanaway gravelly sandy loam, a nearly level to undulating, somewhat excessively drained soil (Zulauf 1979). The surface layer is black gravelly sandy loam, with a dark grayish brown very gravelly sandy loam subsoil (Zulauf 1979). This soil type, with only a few minor inclusions, forms the broad plain between Lakewood and Roy, on which Fort Lewis is located. Early explorers and settlers reported frequent, late-season fires on the prairies and oak woodlands in this region, suggesting that Native Americans set fires to enhance the growth of edible prairie plants and to aid in hunting (Lang 1961, Norton 1979, Boyd 1986).

Fort Lewis is one of several prairies on outwash plains in western Washington. The basic floristic composition of these prairies has been known for years (Jones 1936). The Mima Mound prairie, ~10 km south of Fort Lewis, was studied by del Moral and Deardorff (1976). The flora of this prairie is similar to the prairie on Fort Lewis, although it appears more modified than Fort Lewis prairies. Both prairies are dominated by native Idaho fescue and several native forbs. Camas (*Camassia quamash*) is an indicator species. Both prairies support prominent populations of aliens, especially hairy cats-ear (*Hypochaeris radicata*) and Kentucky bluegrass (*Poa pratensis*). Hairy cats-ear is noteworthy, since it already was conspicuous and abundant in western Washington prairies by the 1930s (Jones 1936).

On Fort Lewis, fire exclusion has allowed 6,560 ha of the original 16,800 ha fescue prairie to be converted to forest since 1870 (Figure 2). Before 1870, fescue prairies were large and interconnected. Currently, only a fraction of the original fescue prairie remains as small, isolated grasslands (Figures 1, 2). Large areas of oak woodland also have been lost to invading Douglas-firs, but past records did not distinguish oak woodlands from conifer forest.

Figure 1. The fescue grassland on Wier Prairie in May 1999. In the left background is a Garry oak woodland and encroaching Douglas-fir forest. In front of these wooded stands is a band of Scot's broom, encroaching on the fescue grassland.

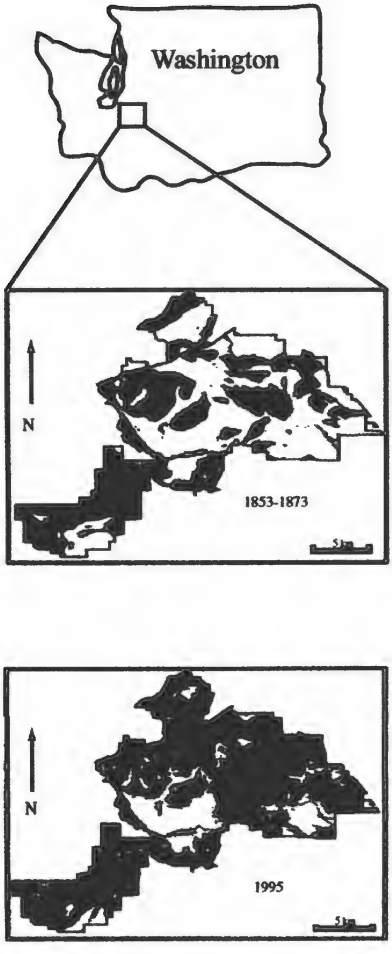

Figure 2. Land cover maps on Fort Lewis, from data provided by Teresa Hansen and Brandy Riche of Fort Lewis. Black depicts the extent of forested areas; white represents prairies. Top: based on 1853-1878 land records. Bottom: based on 1995 land surveys.

Scot's broom (*Cytisus scoparius*) has benefited from fire exclusion by invading many of the remaining prairies and oak woodlands on Fort Lewis (Figure 1). This alien shrub rapidly degrades prairies by forming dense, 1-3 m tall canopies that shade prairie species. Mature broom stands also support high intensity, high severity fires by generating large amounts of woody fuel. Scot's broom is a resprouter, thus all control methods must account for broom persistence after treatment. Broom sprouts are least successful if the treatment is applied during maximum growing season stress (Ussery and Krannitz 1998).

Three fire-management regimes exist on Fort Lewis. The first, and most widespread, is fire exclusion on ~28,000 ha. The second regime comprises a prescribed fire program applied predominantly in spring. Fort Lewis began lighting prescribed fires in the 1960s, and since 1978 has managed a comprehensive prescribed fire program on 3000 ha of prairies and oak woodlands with 3-5 yr rotations. Most prescribed fires are set in February/March, but fires occasionally are set in fall. Wier Prairie, in the southwest corner of Fort Lewis, is in this management regime. The fescue grassland on Wier Prairie is presumed to be the closest approximation to the original prairie community at Fort Lewis, although it contains alien species (Figure 1). Various oak woodlands associated with the prairies are considered to represent a former original component on Fort Lewis. The third fire regime is a 3000 ha artillery impact area on the Ninety-first Division Prairie, where frequent training fires within the prescriptions of the fire management plan are allowed to burn. Bombing is concentrated in a central 1000-1200 ha area, which we call Artillery Prairie. This site has been subjected to broadcast burns ignited by artillery fire nearly annually for 50 yr. Despite the heavy use of fire, no studies have been published on the effects of fire on Fort Lewis prairies and oak woodlands.

Fort Lewis is an excellent site to examine species and community responses to prescribed fire on prairies and oak woodlands. Fort Lewis has three widely divergent, documented fire regimes in a small area with uniform soils, it is the only site in western Washington with a long-standing program of consistent prescribed burning, and it contains many of the largest, highest quality fescue prairies and oak woodlands in western Washington. This study was designed to answer four research questions: 1) what is the current composition of prairies and oak woodlands on Fort Lewis? 2) will prescribed fires maintain the status of prairie and oak woodland species? 3) do species frequency, cover, and recruitment vary between spring and fall prescribed burns? 4) does prescribed fire reduce frequency and density of

invading Douglas-fir, Scot's broom, and other alien species?

Methods

Community Composition

We set prescribed fires in fescue grasslands and oak woodlands, currently managed under the 3-5 yr fire regime, and in broom thickets where prairie fires had partially succeeded in removing Scot's broom. We used the annual broadcast burn at Artillery Prairie as the fire treatment in the cats-ear meadow. Fire effects on herbaceous species were evaluated on alternate 1 x 1 m microplots arranged along transects that varied in length depending on community type. The buffer zones between the 1 m^2 microplots were used to separate the prescribed fire treatments. The distribution of burned microplots in each community is shown in Table 1.

TABLE 1. Distribution of burned plots for understory species in each community exposed to different burn treatments. These plots also contributed to the data on preexisting composition in Table 3.

Community	Fire regime	Burn date		
		Aug 94	Sep 94	Mar 95
Fescue grassland	3-5 yr	-	30	60
Oak woodland	3-5 yr			
Herbaceous		-	33	29
Woody		-	17	13
Cats-ear meadow	Annual	90	-	-
Broom thicket	3-5 yr			
Herbaceous		-	28	5
Woody		-	17	13

Fescue grassland composition was surveyed using 90 microplots on four 40-60 m transects, arranged as two pairs of parallel transects. The 90 cats-ear meadow microplots were placed along one randomly located 180 m transect, 200 m inside the artillery impact area, as dictated by safety restrictions. Microplots for sampling herbaceous species in oak woodlands and broom thickets were located on 3-15 m transects within 44 10 x 20 m macroplots (see below). These transects were short because stands were discontinuous. All oak woodland macroplots were located within 5 m of tree trunks to ensure they measured the maximum effect of tree cover on the understory. All macroplots in broom thickets were located within 5 m of open prairie to ensure that the site had been invaded recently by Scot's broom and that prairie species were still present in the stand.

Fire effects on woody species were determined using 10 x 20 m macroplots in oak woodlands and broom thickets. Garry oak and Scot's broom were surveyed together on the same 44 macroplots placed along a kilometer of prairie-oak woodland ecotone. Nomenclature for vascular species follows Hitchcock and Cronquist (1973). Voucher specimens are housed by the Land Condition Trend Analysis Program on Fort Lewis.

Data on preexisting composition were gathered May-August 1994 on all microplots shown in Table 1, and postfire data were gathered on the same microplots May-July 1995. No 1995 data were gathered in the cats-ear meadow. The site has been subjected to annual broadcast burns for many years, and we presumed that composition has been unchanged for years. We estimated weighted cover, because fire often reduces the thickness of the foliage without changing the canopy spread of the plants. Cover (C′, as canopy coverage) was estimated to the nearest 1%. Foliage density (D) was estimated to the nearest 5%, expressed as a decimal. Weighted cover (C) was calculated as $C = C' * D$. Cover, height, and diameter at breast height were recorded for all oaks and Douglas-firs. After the final inventory, species were classified as fire increasers, fire maintainers, or fire decreasers, based on changes in frequency. Fire increasers gained at least 10 percentage points in frequency from preburn frequency, fire maintainers were within ±10 percentage points of preburn frequency, and fire decreasers lost at least 10 percentage points in frequency from preburn frequency. We chose 10 percentage points so that species with frequencies up to 90% had latitude to increase on the site, and species with frequencies as low as 10% had latitude to decrease. In either case, maintainers were not automatically favored by this choice.

Fire Treatments

We burned 1 m^2 microplots in the grasslands on Wier and Artillery prairies, and 10 x 20 macroplots in the oak woodlands and broom thickets, in September 1994 and March 1995. The 1 m^2 microplots were assigned randomly to the fire treatments (Table 1). Microplots not scheduled to be burned were soaked with water. Scratch

lines were placed around some of the oak and broom macroplots because of high fuel loads. All prescribed fires were set with 10-20°C ambient temperatures and 20-50% relative humidity. Wind speeds were <5 km/h during all fires, except over the fescue grassland in March 1995 when gusts reached 10 km/h, causing fires to escape and burn 60 microplots, rather than the intended 30. Cats-ear meadow microplots were randomly placed in a single broadcast fire set by bombing in August 1994. Fire weather for spring fires was well within the normal weather patterns for prescribed fires. Fall fires, however, were delayed later than planned because summer 1994 was hot and dry for longer than normal. Prescription weather and conditions were met a few days after light rain in early September.

All prairie microplots burned completely. Fires were patchy in the oak woodlands and broom thickets. Most of the unburned area was under a thick broom canopy, where grass cover was low and fuel moisture was high. Flame heights were <1 m in prairie and oak plots, <2 m in broom plots.

Temperatures of Prescribed Fires

Peak fire temperatures were measured using OMEGALAQ temperature-indicating paints that melt at 142°, 246°, 343°, 427°, 538°, and 649°C (Table 2). The range of paints was striped on 3 x 10 cm aluminum plates, then the plates were placed on the ground in each community just before fires were set. The range of temperatures is consistent with low intensity fires. In general, 60-80% of the plates reached 246° to 343° (Table 2). No plate reached 538° or 649°.

Fuel Sampling

Samples of the fuel loads were collected in May 1995 from randomly selected unburned and burned microplots created for the baseline composition survey. Fuel samples were collected from 12 microplots for each treatment in each community. Because of the escaped fire in the fescue grassland in March 1995, however, unburned prairie fuels were collected from 12 microplots randomly placed in an adjacent unburned area. Fuels were separated into live fine fuels (i.e., all live grasses and forbs), dead fine fuels, and dead wood. In the broom thickets, however, it was not feasible to separate dead fine fuels and dead wood because broom produced abundant brittle twigs. All fuel samples were oven-dried at 105°C for 48 hr in a forced-air oven, then weighed. Fuel loads are expressed in kg/ha.

Experimental Design and Statistical Analysis

The data for preburn/postburn treatment comparisons were gathered in a randomized complete block ANOVA design; individual microplots defined the blocks. The data for fall/spring and unburned/burned treatment comparisons were gathered in a completely randomized design ANOVA. For all statistical analyses, the significance level was set at $P = 0.05$ before the research began. Data reported in the tables as percentages were transformed by arcsine before analysis.

TABLE 2. Percent of heat sampling paints burned at different fire temperatures by community type and fire season. Fire temperatures were measured using OMEGALAQ fire sensitive paints on metal plates placed on the ground in each community before the fires were set. No fires reached 538° C

Community	Season	Plates	Temperature (°C)				
			142°	246°	343°	427°	538°
Fescue grassland	Spring	30	43	54	3	-	-
	Fall	30	3	77	20	-	-
Oak woodland							
Tree base	Spring	43	33	39	26	2	-
	Fall	23	16	68	16	-	-
Understory	Spring	34	23	44	30	3	-
	Fall	23	22	65	13	-	-
Cats-ear meadow	Summer	27	71	29	-	-	-
Broom thicket	Spring	15	33	60	7	-	-
	Fall	30	13	44	33	10	-

Results

Preexisting Composition

The fescue grassland on Wier Prairie was dominated by native prairie species, with the exception of hairy cats-ear, English plantain (*Plantago lanceolata*), and colonial bentgrass (*Agrostis tenuis*). Frequencies for the dominant species were high on the prairie, and total cover was >80% (Table 3). Under the current 3-5 yr fire rotation, the bunchgrass Idaho fescue dominated. Hairy cats-ear was the most important prairie forb, but with considerably less cover. Both species were continuously distributed throughout the sample area. Cryptogams, mainly the mosses *Rhacomitrium canescens* and *Polytrichum juniperinum*, were continuously distributed in the prairie, accounting for ~23% cover. Oregon sunshine (*Eriophyllum lanatum*), prairie lupine (*Lupinus lepidus*), field wood-rush (*Luzula campestris*), long-stoloned sedge (*Carex pensylvanica*), and English plantain were nearly continuously distributed with frequencies greater than 80%, but all had low cover values (Table 3). Hounds-tongue hawkweed (*Hieracium cynoglossoides*) and western witchgrass (*Panicum occidentale*) grew contagiously.

Understory cover was <30% in the oak woodlands, and most was accounted for by alien species (Table 3). Under the current 3-5 yr fire rotation, rhizomatous graminoids dominated the understory (Table 3). The four most prominent species, Kentucky bluegrass, long-stoloned sedge, colonial bentgrass, and red fescue (*Festuca rubra*), are rhizomatous. These four species plus suckling clover (*Trifolium dubium*) and English plantain had greater cover in the oak woodlands than in the fescue grasslands (Table 3). Idaho fescue, hairy cats-ear, and Oregon sunshine, the dominant fescue grassland species, were greatly reduced under oaks (Table 3). Except for long-stoloned sedge, frequencies of the species named above differed noticeably between fescue grasslands and oak woodlands. Many other prairie species, such as hounds-tongue hawkweed, prairie lupine, pine

TABLE 3. Percent frequency (F) and mean percent cover (C) of preexisting composition of fescue grassland, oak woodland, cats-ear meadow, and broom thicket species with at least 1% cover in one of the communities. N|A = Native or Alien species.

		Fescue grassland		Oak woodland		Cats-ear meadow		Broom thicket	
Species	N|A	F	C	F	C	F	C	F	C
Festuca idahoensis	N	100	39.9	8	+	8	+	-	-
Hypochaeris radicata	A	100	7.8	51	+	100	19.1	-	-
Luzula campestris	N	98	+	-	-	98	1.3	-	-
Eriophyllum lanatum	N	94	1.7	-	-	-	-	-	-
Lupinus lepidus	N	92	1.4	-	-	-	-	-	-
Plantago lanceolata	A	90	+	44	1.0	-	-	43	+
Carex pensylvanica	N	89	+	92	5.2	20	+	43	1.7
Agrostis tenuis	A	81	+	53	3.7	58	2.1	71	3.0
Panicum occidentale	N	71	1.0	-	-	6	+	-	-
Hieracium cynoglossoides	N	66	2.0	-	-	21	+	-	-
Festuca rubra	N	41	+	24	2.0	98	2.6	-	-
Panicum scribnerrianum	N	12	+	-	-	58	2.0	-	-
Lupinus albicaulis	N	12	1.1	-	-	-	-	-	-
Poa pratensis	A	-	-	98	10.0	-	-	57	2.0
Trifolium dubium	A	-	-	49	1.3	-	-	-	-
Anthoxanthum aristatum	A	-	-	-	-	100	9.8	-	-
Galium parisiense	A	-	-	-	-	-	-	66	2.8
Cytisus scoparius	A	-	-	-	-	-	-	100	61.6
Cryptogams		100	22.6	15	+	100	9.4	43	1.9
Total number of species		52		61		34		37	
Total vascular cover		61.1		25.1		39.0		12.2	
Total cryptogam cover		22.6		0.4		9.4		1.9	

+: <1% cover

lupine (*Lupinus albicaulis*), and western witchgrass, were absent. Few woody species grew in the oak woodlands, and cryptogams were a minimal component of the understory (Table 3).

The annual training-caused fires on the cats-ear meadow have resulted in <50% total plant cover. Most of the cats-ear meadow cover consisted of alien species, but many native species were present as subordinate members of the community. Hairy cats-ear and sweet vernal grass (*Anthoxanthum aristatum*) dominated, and both were continuously distributed in the community (Table 3). Sweet vernal grass is an alien annual, absent in the fescue grasslands and uncommon anywhere on Fort Lewis except Artillery Prairie. Several native, but subordinate graminoids, including red fescue, Scribner witchgrass (*Panicum scribnerianum*), and field wood-rush were favored by annual burning, as indicated by high frequencies. They were contagiously to continuously distributed in the prairie. Frequency of most prairie species was significantly lower in the cats-ear meadow than the fescue grassland, and many species were absent. Idaho fescue was merely a minor component in the cats-ear meadow.

Scot's broom invasion decimates native prairie cover, because canopy cover is so high. Scot's broom was the only continuously distributed species in these thickets (Table 3). All native prairie species were significantly reduced or absent in the broom thickets. Except for long-stoloned sedge, all other understory species were alien grasses and forbs (Table 3). Colonial bentgrass, Kentucky bluegrass, and long-stoloned sedge were the dominant graminoids; wall bedstraw (*Galium parisiense*), an alien annual, was the dominant forb. All had inordinately low cover. Many bare areas existed in the thickets, because of the dense broom canopy.

Prescribed Fire in Fescue Grassland

Six species prominent in the fescue grassland (Table 3) were fire maintainers (Table 4). Idaho fescue, hairy cats-ear, and Oregon sunshine, the three most important species, and the cryptogams maintained high frequency in both fall and spring burns. Cryptogam cover increased significantly in both burns, whereas cover for Idaho fescue and hairy cats-ear decreased significantly (Table 4). Although both burn treatments significantly reduced the cover of the dominant fescue, no plants were killed. Conversely, hairy cats-ear individuals were killed. The high frequency and cover values (Table 4) are accounted for by dense postfire seed germination and growth. Field wood-rush and prairie lupine were classified as decreasers in response to the spring fire only. After both treatments, cover for field wood-rush increased as a result of a flush of post-fire growth. Nearly all prairie lupine plants were killed by the fires, so that the postfire values shown in Table 4 were contributed by recent germinants. Subordinate species in the fescue grassland, but unlisted in Tables 3 or 4, were not affected by fire. They maintained their prefire status, regardless of fire season. Camas, despite low mean cover, is in this category.

TABLE 4. Percent frequency and mean percent cover of fescue grassland species with at least 1% cover in one of the treatments, in response to fall and spring prescribed burns. Species cover values with unlike superscripts between pre- and postburn, by fall or spring burn, are significantly different. Similarly, cover values lacking superscripts are not significantly different. N|A = Native or Alien species.

		Frequency				Cover			
		Fall burn		Spring burn		Fall burn		Spring burn	
Species	N|A	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Maintainers									
Cryptogams		100	100	100	100	25.1[a]	37.5[b]	21.5[a]	26.4[b]
Festuca idahoensis	N	100	100	100	100	40.8[a]	11.7[b]	39.4[a]	9.1[b]
Hypochaeris radicata	A	100	100	100	100	7.9[a]	4.5[b]	7.7[a]	5.7[b]
Eriophyllum lanatum	N	93	97	93	95	1.8	1.4	1.7	1.2
Panicum occidentalis	N	73	63	70	65	0.9	0.6	1.0	0.8
Hieracium cynoglossoides	N	70	70	63	58	2.4	3.1	1.8	2.0
Decreasers in spring burn									
Luzula campestris	N	100	100	98	80	0.6[a]	1.1[b]	0.4[a]	0.7[b]
Lupinus lepidus	N	87	97	95	78	1.3[a]	0.4[b]	1.5[a]	0.3[b]

TABLE 5. Percent frequency and mean percent cover of oak woodland species with at least 1% cover in one of the treatments, in response to fall and spring prescribed burns. Species cover values with unlike superscripts between pre- and postburn treatments, by fall or spring burn, are significantly different. Similarly, cover values lacking superscripts are not significantly different. N|A = Native or Alien species.

		Frequency				Cover			
		Fall burn		Spring burn		Fall burn		Spring burn	
Species	N|A	Pre	Post	Pre	Post	Pre	Post	Pre	Post
					Maintainers				
Poa pratensis	A	91	100	100	90	9.7[a]	6.0[b]	8.2	6.3
Trifolium dubium	A	48	58	59	55	1.9	1.7	1.2	0.6
Hypochaeris radicata	A	48	48	69	72	0.8	1.0	0.8	1.0
Plantago lanceolata	A	39	42	62	66	0.5	1.0	0.8	1.0
Festuca rubra	N	24	27	38	35	0.9	0.9	1.4	1.7
Vicia sativa	A	21	30	41	38	0.1	1.1	0.4	0.4
					Increaser in fall burn				
Carex pensylvanica	N	88	100	100	90	6.4	9.1	4.6	4.7
					Decreaser in spring burn				
Agrostis tenuis	A	61	58	76	59	3.1	1.9	9.0	7.1

Prescribed Fire in Oak Woodlands

Five of the six maintainers in oak woodlands were aliens (Table 5). Two understory species in the oak woodlands responded appreciably to fire, but only in terms of changes in frequency. Colonial bentgrass was a decreaser in the spring burn treatment, whereas long-stoloned sedge was an increaser in the fall burn treatment (Table 5). Kentucky bluegrass, in the fall burn treatment, was the only species with a significant change (decrease) in cover for either treatment.

Prescribed Fire in Broom Thickets

The fall fire burned significantly more of the stand, caused significantly greater mortality, and resulted in significantly less resprouting of broom plants than the spring fire (Table 6). The fall fire resulted in significantly less density and cover of mature broom plants, had no significant effect on seedling density (Table 6), and significantly reduced postfire cover of small broom plants (Table 7). The patchy spring fire significantly reduced postfire seedling density, but had no other significant effects (Table 6). We classified Scot's broom in the understory as a decreaser, although postfire frequency was merely four percentage points less than prefire frequency (Table 7). When all data from Tables 6 and 7 are viewed together, Scot's broom prominence on the site decreased because of fire.

TABLE 6. Effects of Sep 94 and Mar 95 burns on Scot's broom. Postfire data were gathered in May 95 for both burns. Values with unlike superscripts (a-b) are significantly different between fall and spring burns. Values with unlike subscripts (c-d) are significantly different between pre- and postburns, by fall or spring burns. Similarly, values lacking superscripts are not significantly different.

	Fall burn		Spring burn	
Category	Pre	Post	Pre	Post
Area burned (%)		90[a]		78[b]
Stem density per m^2	52.9[c]	11.4[d]	58.2	51.0
Cover (%)	24.8[c]	3.5[d]	13.8	12.0
Seedling density (per m^2)	8.2	5.9	6.3[c]	3.0[d]
Mortality (%)		87.0[a]		47.2[b]
Basal sprouting (%)		1.8[a]		30.8[b]

Cryptogams also were decreasers, losing 30 percentage points of prefire frequency. Except for the maintainer Kentucky bluegrass, all other understory species in the broom thickets were increasers with fall fire (Table 7). Five of the six increaser species were aliens, and all occupied areas that had been bare under the complete broom canopy before the fire. Other species in the broom thickets, unlisted in Table 7, maintained their status with the fall burn treatment.

Fire Effects on Trees

Fire dramatically affected oak stems <1 m tall or <2 cm dbh. The fall fires top-killed more oaks

TABLE 7. Percent frequency and mean percent cover of broom thicket species with at least 1% cover, in response to a Sep 94 prescribed burn. Species cover values with unlike superscripts between pre- and postburn are significantly different. Similarly, cover values lacking superscripts are not significantly different. N|A = Native or Alien species.

Species	N|A	Frequency		Cover	
		Pre	Post	Pre	Post
			Maintainer		
Poa pratensis	A	44	41	2.0	1.4
			Increasers		
Teesdalia nudicaulis	A	19	93	<0.1[a]	1.5[b]
Agrostis tenuis	A	81	100	1.8	5.2
Galium parisiense	A	57	93	1.2	1.5
Carex pensylvanica	N	44	56	2.7	3.0
Hypericum perforatum	A	81	93	1.1	1.9
Plantago lanceolata	A	44	64	0.6	0.4
			Decreasers		
Cryptogams		56	26	2.0	0.5
Cytisus scoparius	A	100	96	62.8[a]	1.9[b]

TABLE 8. Height and diameter classes of Garry oaks top-killed by fall and spring prescribed fires.

	Fall		Spring	
	Prefire density	Number top-killed	Prefire density	Number top-killed
Stem height (m)				
< 1	82.5	77.4	54.8	44.5
1-2	5.7	2.4	6.7	1.6
2-3	3.9	0.7	4.1	0.2
3-4	1.2	0.1	8.0	0
> 4	8.4	0	8.0	0
Stem diameter (cm)				
< 2	85.9	76.1	60.8	35.7
2-5	3.4	0.1	4.4	0.2
5-10	4.3	0.1	3.8	0
> 10	5.6	0	5.4	0

than the spring fires in these height/diameter classes (Table 8). Oak mortality from fire was trivial. Of the prefire densities shown in Table 8, only three <1 m tall sprout clumps, with 5-10 stems each, and two of the 5-10 cm dbh trees were killed by fire. Otherwise, all top-killed stems resprouted. Taller and larger diameter trees were unaffected by fire.

Spring fire significantly reduced Douglas-fir from 13.9 to 4.5 stems/ha for saplings <1 m tall, and from 21.3 to 10.6 stems/ha for saplings <2 cm diameter. No Douglas-firs >3 m tall or >5 cm diameter were killed by fire.

Fire Effects on Fuels

Compared to the unburned condition, both fall and spring fires significantly reduced total fuel loading (Table 9). Fuel loadings were lowest in fescue grasslands and highest in oak woodlands. There was no significant difference in fuels after fall and spring fires in fescue grasslands. Fall and spring fires significantly reduced total fuels in the oak woodlands, mainly by reducing dead fine fuels. Fall fires in the broom thickets significantly reduced total fuels, but spring fires failed to carry through broom thickets.

TABLE 9. Fire effects on total fuel loading (kg/ha) in fescue grassland, oak woodland, and broom thicket. Both fall and spring burns significantly reduced the total fuel loading in each community, compared to the unburned condition.

	Unburned	Fall	Spring
Fescue grassland	1702	0	0
Oak woodland	3694	2345	1929
Broom thicket	2804	1847	-

Discussion

All fires in this study favored prairies and oak woodlands by killing invading Scot's broom and Douglas-fir (Tables 4-7). Prairie species are fire endurers, so that prescribed fires did not damage the fescue grassland, regardless of fire season (Tables 3, 4). The present species composition in the fescue grassland has been maintained using prescribed fires for 20 yr. Prescribed fires temporarily reduced Idaho fescue cover, had no significant effect on frequency, and did not remove Idaho fescue as the dominant prairie species. Prescribed fires caused no significant changes to most native or alien subordinates, nor to community composition. Furthermore, prescribed fires maintained open Garry oak stands by top-killing Garry oak saplings and seedlings, reducing Scot's broom cover, and killing young Douglas-firs.

Fire regimes shorter or longer than the 3-5 yr fire rotation on Fort Lewis have been shown to be deleterious to prairies and oak woodlands (Table 3). Excessive burning harms most native prairie

species. Fifty years of annual broadcast burning changed 1000-1200 ha of Artillery Prairie from a community dominated by perennial bunchgrasses to one dominated by alien forbs and annual grasses (Table 3). Compared to the fescue grassland, native plant cover was significantly lower, and community composition was dramatically altered. The displacement of Idaho fescue as the dominant species and the presence of many alien species indicated that the native prairie community is not adapted to prolonged annual burning. Annual burning, however, has maintained graminoid and forb dominance by eliminating Scot's broom and restricting invasion/establishment by Douglas-fir.

Compared to excessive burning, however, fire exclusion affects a much greater area on Fort Lewis. Fire exclusion has allowed Scot's broom and Douglas-fir to invade prairies and oak woodlands (Figure 1). Closed stands of Scot's broom and Douglas-fir eliminate nearly all native prairie species; closed canopies within Douglas-fir forests eliminate both prairie and oak woodland species.

Most prescribed fire programs strive to promote grassland and savannah structures by limiting the stem density of woody species. In general, prairie fires initially reduce graminoid cover (Nimir and Payne 1978, Antos et al. 1986) or biomass (Ewing and Engle 1988), promote rapid herbaceous postfire growth (Antos et al. 1986), and have positive effects (or no effect) on frequency of the native prairie species (Anderson and Bailey 1980, White 1983, Wilson and Shay 1990). The prairies on Fort Lewis responded exactly in this manner to prescribed fires.

Prescribed fires on Fort Lewis resulted in topkill and triggered resprouting for small Garry oak individuals, but caused no damage to mature trees. These responses to fire are common in many oaks. Some of the well-known oak species that endure fire by resprouting are blue oak (*Quercus douglasii*), scrub oak (*Q. dumosa*), and interior live oak (*Q. wislizenii*) in California (Allen-Diaz and Bartolome 1992, Keeley 1992); Gambel oak (*Q. gambelii*) in Arizona (Harrington 1985); myrtle oak (*Q. myrtifolia*), sand live oak (*Q. geminata*), turkey oak (*Q. laevis*), bluejack oak (*Q. incana*), and sand post oak (*Q. margaretta*) in Florida (Guerin 1993, Glitzenstein et al. 1995); jack oak (*Q. ellipsoidalis*) and bur oak (*Q. macrocarpa*) in Minnesota (White 1983); and white oak (*Q. alba*), black oak (*Q. velutina*), and chestnut oak (*Q. prinus*) in New Jersey (Boerner 1981).

Some fire effects on Fort Lewis differed from results observed elsewhere. Fires were followed by higher forb cover in California prairies and oak woodlands (Heady 1972, Sugihara and Reed 1987), Montana prairies (Antos et al. 1986), and Minnesota oak savannas (White 1983), but not in corresponding communities on Fort Lewis. Likewise, cryptogam cover was lower after fire in Montana prairies (Antos et al. 1986), compared to higher cryptogam cover after fires in fescue grassland.

Our research indicates that fire is essential in maintaining prairie and oak woodland communities in western Washington. Early explorers and settlers noted a high incidence of fire on prairies (Lang 1961, Norton 1979, Boyd 1986), and prairie covered more area in the mid-1800s than currently (Figure 2). Excluding fires since the early 1900s has allowed Douglas-fir to invade prairies and oak woodlands, suggesting that fire once helped maintain the more open communities (Figures 1, 2). The situation at Fort Lewis is identical to the Mima Mound prairie, where Douglas-fir invasion has changed prairie species adapted to xeric, low fertility soils to forest species adapted to mesic, more fertile soils (del Moral and Deardorff 1976). At least one of the contributors to better nutrient inventory is Scot's broom, a known nitrogen-fixer (Ussery and Krannitz 1998).

On Fort Lewis, only frequently burned areas have continued to support large prairies and open oak woodlands (Tables 3-5). The current prescribed burning program, however, must be expanded to reverse prairie loss to Scot's broom and Douglas-fir. This study has shown that fall fires killed more Scot's broom and Douglas-fir than spring fires, but fall fires had nearly the same beneficial effects (e.g., reducing fuels, maintaining species) as spring fires on prairies and oak woodlands. A program based on fall fires could help remove Scot's broom and Douglas-fir from heavily invaded sites. The exact timing of fire in broom thickets determines how successfully the program will work. Although Scot's broom resprouts, stems of all diameters resprout less successfully after mid-summer cutting (Ussery and Krannitz 1998). On the other hand, broom seeds mature in mid-summer (Ussery and Krannitz 1998), so that postfire germination in response

to a late-summer or early-fall fire could repopulate the site with broom seedlings. Using a model of fire in California mixed-conifer forest, van Wagtendonk (1983) showed that more than one prescribed fire cycle is likely to be required to restore the balanced fire regime. We anticipate that multiple fires will be necessary on Fort Lewis. Already, second fires are needed to kill dense broom reproduction before seed crops can be produced in the second postfire growing season. A strategy of aggressive mechanical or chemical removal of Scot's broom, Douglas-fir, and other prominent invaders should supplement prescribed burning to help restore prairies and oak woodlands to the open, historical condition. Given the number of alien species on the prairies (Tables 3-6), many of which have been around for decades (Jones 1936), supplemental seeding and planting of native species may be needed. Once the balanced condition of native prairie species has been achieved, both fall and spring prescribed fires should effectively maintain these communities.

Acknowledgements

It is a pleasure to thank Fort Lewis for funding this research (WAFO-081094). We are indebted to Joe Reasoner, John McGuire, Charlie Askins, Lori Belanger, and Inger Schmidt for helping with various aspects of the prescribed fires. Teresa Hansen and Brandy Riche provided the basic figures from which Figure 2 was constructed by Jeannie Gilbert. David L. Peterson and an anonymous reviewer provided useful criticism that improved the manuscript.

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Received 8 March 1999
Accepted for publication 7 June 1999

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Effects of Timber Harvest on *Cimicifuga elata,* a Rare Plant of Western Forests

Abstract

Cimicifuga elata (tall bugbane) is a Species of Concern with the U.S. Fish and Wildlife Service and it is considered by Natural Heritage programs in Oregon and Washington to be endangered. Since the species occurs in forests, its conservation could conflict with other forest uses such as timber harvest. It has been postulated that the species is dependent on old-growth coniferous forests. The objectives of this study were to compare populations of this species among sites with differing forest-management histories. In contrast to previous reports, we found that *C. elata* in uncut old-growth forest was smaller and less reproductive than in clearcuts, probably because plants responded well to additional light in cut-over areas. Plants in areas with other management histories, such as second growth and thinned stands (both >70 years old), were intermediate in size. Population structure also differed among management types. Herbivory by deer and elk was more frequent in clear cuts and edges than in unmanaged old-growth forests. No populations were known at the time of this study from second growth forests of moderate age (20-30 years), and it is possible that competing vegetation excludes *C. elata* from clearcuts after a few years. Management actions that retain hardwoods, thin stands, or create gaps may improve at least short-term conditions for this species.

Introduction

Timber harvest is a widespread disturbance of forest ecosystems in western Oregon and Washington. According to most estimates, less than 20% of old-growth forest present in the 1880's remains, and these forests are now highly fragmented (Spies and Franklin 1988, Norse 1990). Environmental conditions on the forest floor change substantially when forests are clearcut. Compared to old-growth Douglas-fir forests, for example, clearcuts have lower humidity and higher soil and air temperatures, short-wave radiation, and wind speed (Chen et al. 1993, 1995). In addition, some forest harvest practices can cause soil compaction and erosion (Worrell and Hampson 1997), and change nutrient balances (Knoepp and Swank 1997). Not surprisingly, because of extreme changes in physical and site conditions, removal of overstory trees may reduce understory diversity and negatively affect the abundance of some common forest herbs (Halpern and Spies 1995).

Rare plants frequently have narrow geographic ranges, small population sizes, and/or restricted habitat requirements (Rabinowitz 1981, Rabinowitz et al. 1986), characteristics that may inhibit their recovery from disturbance. In a recent study of a highly disturbed landscape, for example, Fischer and Stocklin (1997) showed that local extinction was most likely for plants with small populations or high habitat specificity. Populations of rare species in ancient forests may be threatened by logging practices that damage established plants and alter habitat conditions. An estimated 38% of rare vascular plants in Oregon are thought to be threatened by logging and associated activities (Kaye et al. 1997), but few studies have quantified the effects of timber harvest on populations of these species.

Cimicifuga elata (tall bugbane) is a plant of forested habitats west of the Cascades in Oregon, Washington, and British Columbia. It is considered endangered by both the Washington (1997) and Oregon (1998) Natural Heritage programs, and it is a U.S. Fish and Wildlife Service Species of Concern (formerly a C2 candidate for listing as threatened or endangered). The presence of the species in federally managed forests, especially in proposed timber sales, creates the potential for population loss due to logging effects (USDA 1994, 1996). Information on how this species responds to forest harvest is, therefore, crucial for its long-term conservation. Previous reports suggested that populations of *C. elata* in or near clearcuts may have reduced vigor compared to those in unmanaged forests (Alverson

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1986), and the same concern has been expressed for *C. laciniata* (cut-leaved bugbane), a related species of northwestern Oregon forests (Siddall and Brown, 1990). The goals of this study were to document differences in *C. elata* plant size and fecundity, population structure, and herbivory in populations with varied histories of timber harvest throughout the geographic range of the species.

Study Species

Cimicifuga elata is an herbaceous perennial in the Ranunculaceae (buttercup family). It produces sprays of white, apetalous flowers and has a self-compatible, facultatively geitonogamous mating system (Pellmyr 1986a, Evans 1993). The genus as a whole includes 15 species world wide (Mabberley 1993) and has been the focus of research on pollination ecology (Pellmyr 1985, 1986a, Evans 1993), evolution and systematics (Pellmyr 1986b, 1986c, 1987; Ramsey 1965, 1986, 1987; Groth et al. 1987, Compton 1998), seed germination (Baskin and Baskin 1985), and pharmacology (e.g., Shibata et al. 1975, 1977, 1980). Over the majority of its range, *C. elata* occurs on moist north-facing slopes in mixed conifer/hardwood forests, with a canopy dominated by *Pseudotsuga menziesii* (Douglas-fir) and *Acer macrophyllum* (big-leaf maple) (Kaye and Kirkland 1994).

Populations of *Cimicifuga elata* are generally small; more than half have fewer than twenty-five individuals (Kaye and Kirkland 1994). In the United States, the species occurs from northern Washington to southern Oregon, entirely west of the Cascade Range (Figure 1). In Oregon, it is found on federal lands of the Mt. Hood, Willamette, and Umpqua National Forests; the Salem, Eugene, Roseburg, and Medford Districts of the Bureau of Land Management; and Army Corps of Engineers properties associated with dams and reservoirs in the Cascade Range. In addition, a few populations are known from state forests, state and county road rights-of-way and parks, and private lands (Kaye and Kirkland 1994).

Methods

To evaluate the effects of forest management on *Cimicifuga elata*, we conducted an observational study of populations with various land-use histories from northern Washington (Olympic Peninsula) to southern Oregon, and concentrated in western Oregon between the Columbia Gorge and Lane County (Figure 1). Information detailing the location of known sites was obtained from the Oregon and Washington Natural Heritage Programs and federal agencies. Populations included in this study ranged in size from 3 to 103 individuals, and averaged 35 plants. Thirty-seven populations were visited in 1992 and 24 of these were revisited in 1993. The land-use histories of these populations fell into six management categories. Ranked from least to most disturbed, these categories were: unmanaged (often old-growth), selectively thinned (more than 70 years ago), second growth (greater than 70 years old), edge between recent clearcut and unmanaged forest (within 15-m either side of edge), recent clearcut (less than five years old), and roadside. Of the 37 study sites visited in 1992 (and 24 resampled in 1993), 15 (8) were undisturbed, 5 (4) thinned, 3 (3) second growth, 4 (4) edges, 4 (3) clearcut, and 6 (2) roadside. Field work took place between late June and early August of both years.

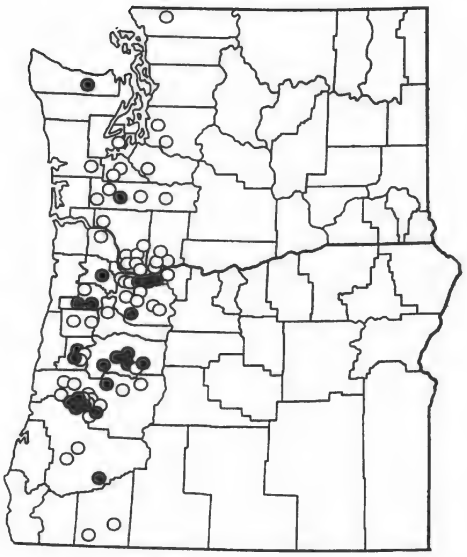


Figure 1. Distribution of *Cimicifuga elata* in Oregon and Washington. Solid dots indicate populations included in this study. Some overlapping dots were omitted to improve clarity.

At each site, individual *Cimicifuga elata* plants were evaluated for height, number of flowering racemes, and area of the largest (usually lowest) leaf. The tripartite leaves of *C. elata* are roughly

triangular, so leaf area was estimated from measurements of leaf length and width, and calculated as length × width × 1/2. We measured all individuals at most populations. In six cases, however, a large sample of individuals (a census of the largest subpopulation) was measured because the populations were so large or scattered that all portions were difficult to reach. Evidence of herbivory by deer or elk was also recorded at 27 and 16 of the sites in 1992 and 1993, respectively. Herbivory was attributed to deer and/or elk based on observations of bite style; cropped stems were broken or torn, which results from the lack of upper incisors in these ungulates (Anderson 1969, Dolbeer et al. 1994). Domestic livestock, which may also leave this type of evidence, were not present at these sites.

We used one-way Analysis of Variance (ANOVA; STSC, Inc. 1991) to test the null hypothesis that management history had no effect on plant height, number of racemes, and frequency of herbivory in 1992 and 1993. Only reproductive plants were considered in tests with the first two response variables to minimize the effects of population structure (which were tested separately, see below), and, in the case of raceme number, improve the fit of our data to a normal distribution. If all plants were included, populations with high proportions of small, newly recruited plants might not be distinguished from those with a high proportion of mature plants with low vigor. Consideration of reproductive plants only reduced sample sizes for some treatments because reproductive plants were absent from some populations. Data for frequency of herbivory were log transformed (after addition of 0.5 to all values) to meet the assumptions of normality and equal variances required by ANOVA. Fisher's Protected LSD was used to compare means (STSC, Inc. 1991) because it is relatively robust to unequal sample sizes.

Finally, we assigned each individual to one of three life-history categories to investigate the effects of timber harvest on population structure. Plants were considered reproductive if they flowered (produced one or more racemes). Non-reproductive plants with area of the lowest leaf >611 cm^2, which was one standard deviation below the 1992 pooled mean for reproductive plants ($\bar{x}$=1311 cm^2, S.D.=700 cm^2, n=380), were arbitrarily classified as medium-sized. Small plants were defined as non-reproductive plants with a leaf area ≤611 cm^2. The importance of identifying medium-sized plants is that they may represent suppressed individuals that are big enough to reproduce but lack sufficient resources, such as light, to flower.

We tested the null hypothesis that the abundance of plants in each stage was independent of management history in 1992 and 1993 using a generalized linear model procedure in SAS (proc genmod; SAS Institute, Inc. 1990). In this analysis, the log of the mean was linearly related to the treatments and variance was Poisson distributed. This loglinear model is appropriate for count data of individuals in different categories (Steel, Torrie, and Dickey, 1997), such as size classes and treatments. A scale parameter was included in the model to allow for greater variation than expected (over-dispersion) from a Poisson distribution, and total population size was included as an offset term to remove effects of population size. To illustrate population structure, we calculated the relative frequency of each life-history stage within each population and estimated the mean and standard error for each treatment. Analyses performed for each response variable are summarized in Table 1, along with the sample size for each management history category in each test and year.

Results

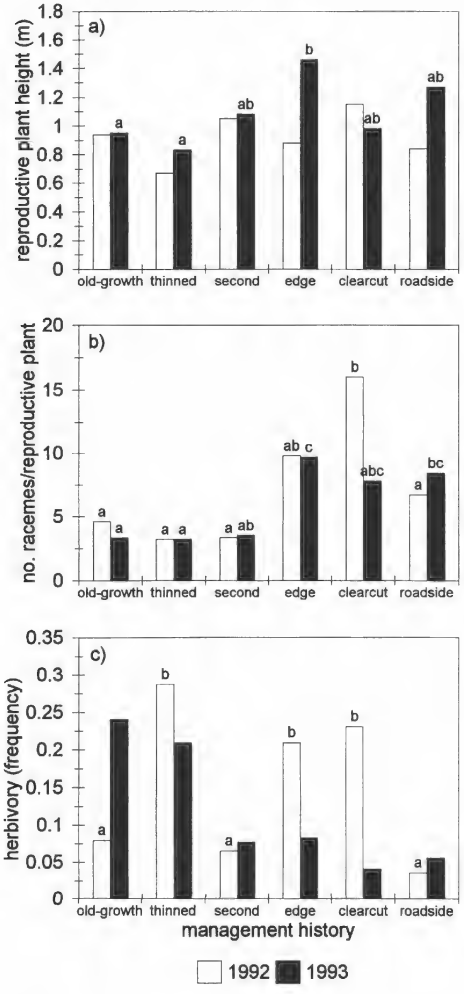
Plant Size and Reproduction

Average reproductive plant size and inflorescence production differed significantly among forest management types, but some of these effects were significant in only one year. Mean height of reproductive plants, for example, differed among forest management types in 1993 ($F_{5,14}$=4.027, P=0.018), but not in 1992 ($F_{5,23}$=1.706, P=0.173). In 1993, plants along clearcut-forest edges were significantly taller (by about 60%) than those in unmanaged forests or selectively thinned stands, while plants in other management types had intermediate heights (Figure 2a).

Management history had a significant effect on average number of racemes per reproductive plant in 1992 ($F_{5,23}$=2.563, P=0.050) and 1993 ($F_{5,14}$=3.698, P=0.024). In 1992, mean inflorescence production was greater in clearcuts ($\bar{x}$=16 racemes per reproductive plant) than in unmanaged forests, selectively thinned stands, second growth, or roadsides (mean range: 3.2-6.7). Raceme pro-

TABLE 1. Dependent variables, analyses and sample sizes for each management history category (independent variables) in 1992 and 1993.

Dependent variable	Reproductive plant height	Racemes/repro. plant	frequency of herbivory	population structure
Analysis:	one-way ANOVA	one-way ANOVA	one-way ANOVA	loglinear analysis
	Sample sizes (1992/93)			
old-growth	11/7	11/7	11/3	15/8
selectively thinned	4/4	4/4	4/3	5/4
second growth	2/2	2/2	3/2	3/3
edge	3/3	3/3	4/3	4/4
recent clearcut	3/2	3/2	3/3	4/3
Roadside	6/2	6/2	4/2	6/2
N	29/20	29/20	27/16	37/24



duction was significantly higher along edges ($\bar{x}$=9.7 racemes) than in unmanaged or thinned forests ($\bar{x}$=3.3 and 3.2 respectively) in 1993 (Figure 2b).

Herbivory

The frequency of herbivory also differed significantly among management histories, but only in 1992 (1992: $F_{5,23}$=7.749, P=0.0003; 1993: $F_{5,10}$=1.039, P=0.446). Herbivory in unmanaged forests, second growth and along roadsides (mean range: 3.4-7.9%) was substantially less than in selectively thinned stands, edges, and clearcuts (mean range: 21-29%, Figure 2c).

Population Structure

Population structure differed among the six forest management types, especially in 1993. Treatment effects in the loglinear models have F=0 and P=1 because total population size was held constant as an offset in the models, making the stage×treatment interaction the effect of interest in this case. Model terms for the interaction between stage and management history in the loglinear analyses (Table 2) were weak in 1992 (P=0.0883) and significant in 1993 (P=0.014).

← Figure 2. Mean reproductive plant height (a), number of racemes (b), and frequency of herbivory (c) in six categories of forest management history in 1992 and 1993. See text for explanation of categories. Means with the same letter in the same year did not differ at the 0.05 level of probability (Fisher's protected LSD); letters are not shown for years where ANOVA did not detect a treatment effect. Herbivory data were log-transformed prior to analysis. See Table 1 for sample sizes.

TABLE 2. Effect of management history on the number of individuals in three life-history stages (small vegetative, medium vegetative, and large reproductive) examined by loglinear analysis with data from 1992 and 1993. Numerator and denominator degrees of freedom (NDF and DDF, respectively) are shown for each *F*-ratio.

Source	NDF	DDF	*F*	*P*
1992				
Stage	2	93	16.7088	0.0001
Treatment	5	93	-0.0000	1.0000
Stage*Treatment	10	93	1.7168	0.0883
1993				
Stage	2	54	35.0175	0.0001
Treatment	5	54	-0.0000	1.0000
Stage*Treatment	10	54	2.5316	0.0140

These interactions indicate that the relative number of individuals in each stage depended on management history in 1993 and nearly so in 1992.

In general, populations in all forest management types were dominated by small vegetative plants, except for populations along roadsides, which tended to have few small individuals and a relatively high frequency of reproductive plants (Figure 3). Populations in unmanaged forests and second growth generally had proportions of medium-sized vegetative plants approximately equal to or higher than reproductive plants. For example, the average fraction of medium-sized plants in these management types in 1992 ranged from 27% to 40%, while reproductive plants averaged only 19% to 26% in the same habitats and year. In contrast, reproductive plants tended to outnum-

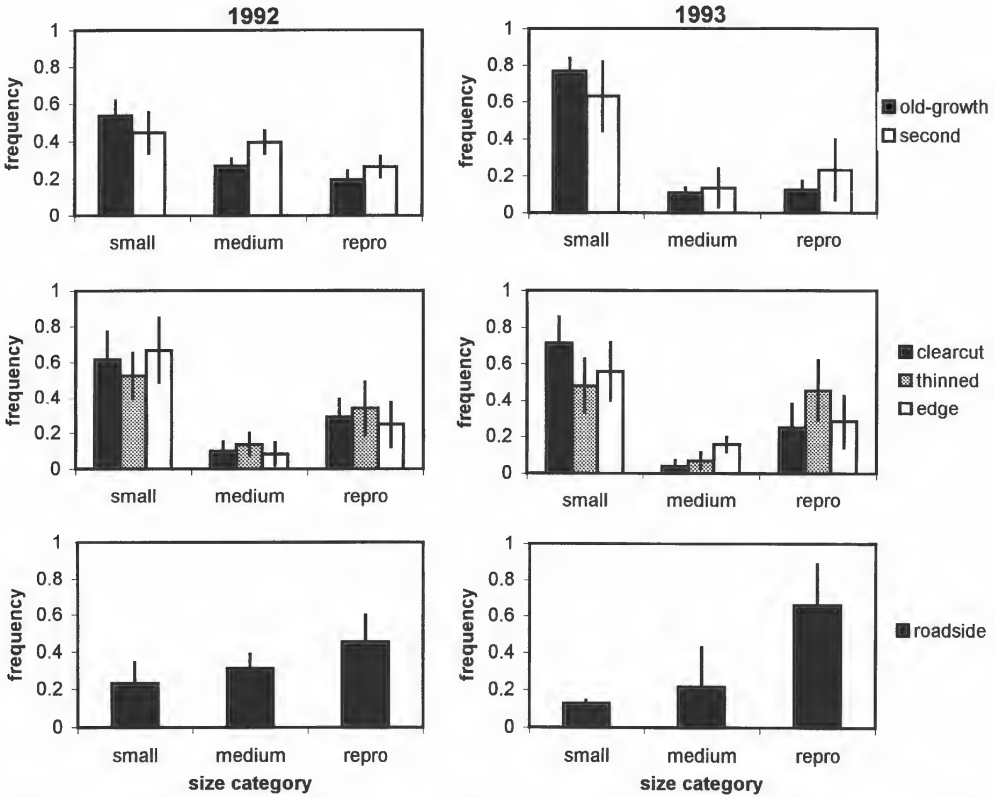


Figure 3. Relative frequency (±1 SE) of life-history stages within each management treatment in 1992 and 1993. Treatments are grouped by types that follow similar patterns. See Table 1 for sample sizes.

ber medium vegetative plants in selectively thinned stands, edges, and clearcuts. Populations in clearcuts, for instance, averaged 29% reproductive plants in 1992 and 24% in 1993, while medium-sized plants made up only 10% and 4%, respectively, of the same populations. On average, roadside populations were dominated by reproductive plants ($\bar{x}$=45% and 66%), with respectively lesser amounts of medium ($\bar{x}$=31% and 21%) and small vegetative individuals ($\bar{x}$=23% and 13%).

Discussion

This study detected differences among various habitat-management histories at the level of individuals and populations. *Cimicifuga elata* plants in unmanaged, old-growth forests and mature second growth stands tended to be smaller with fewer racemes than those in some types of disturbed forests, but these differences varied with year of observation. For example, reproductive plants in unmanaged areas were shorter (in 1993) than those along old-growth-clearcut edges, and they had fewer inflorescences than plants in clearcuts (1992) or along edges and roadsides (1993). Population structure also differed among forest management types, especially in 1993. The added light (and possibly heat) reaching plants in thinned stands, edges, and especially clearcuts may have been responsible for their greater size and fecundity, but additional study will be required to test this hypothesis and determine the importance of other resources, such as nutrients and water, as factors controlling the response of this species.

Ecological Implications

These results are inconsistent with the view that *Cimicifuga elata* is old-growth dependent. Instead, the species appears representative of what Collins et al. (1985) termed "light-flexible herbs," which tolerate full sun and shade, but are restricted to neither. Such species respond to canopy disturbances and gaps with increased flowering, seed production, seedling recruitment, and survivorship (Collins et al. 1985, p. 233), largely due to increased light availability. In several respects, *C. elata* is typical of shade-tolerant herbs of temperate deciduous-forests. It is self-compatible and frequently pollinator limited (Pellmyr 1986a), reproduces mainly by seed, lacks specialized seed dispersal appendages (such as pappus or barbs), requires cold stratification for seed germination (Kaye, unpub. data), and generally occurs in populations dominated by small plants, all traits typical of shade-tolerant herbs of eastern North American deciduous forests (Bierzychudek 1982). Seeds of shade-tolerant species are generally heavier than light-demanding herbs (Salisbury 1942), and the seeds of *C. elata* are relatively heavy. The mean dry weight of *C. elata* seeds is 1.9±0.28 mg (Kaye, unpub. data), which is typical of shade tolerant herbs (Bierzychudek 1982) and other species of *Cimicifuga*, such as *C. racemosa* (Abrahamson 1979). These characteristics, combined with our observations of increased size and fecundity in artificial gaps, such as clearcuts, supports the classification of *C. elata* as light-flexible rather than shade restricted (Collins et al. 1985).

Hardwood tree species in western forests of Oregon and Washington are often invaders of moist gaps in coniferous forests (Franklin and Dryness, 1973) because they require the additional light and release from competition available in these sites. The near-constant association of *Cimicifuga elata* with deciduous trees (Kaye and Kirkland, 1994) suggests that it, too, may invade and persist in hardwood-dominated gaps. Hardwoods allow substantial light penetration through the canopy to the forest floor in early spring, prior to leaf expansion (Boyd and Matt 1977), possibly enabling *Cimicifuga* plants to grow rapidly early in the season while moisture is plentiful. If this hypothesis is correct, it may represent a strategy selected in ancestors of *C. elata* from eastern North America. *Cimicifuga* species of that region (including *C. rubifolia*, the closest relative of *C. elata* [Compton et al. 1998]) currently occur in deciduous forests. The fact that medium-sized vegetative plants outnumbered reproductives in uncut stands (at least in 1992, Figure 3) while the reverse was true in disturbed forests may indicate that vegetative plants, though suppressed under a closed canopy, can become reproductive when the canopy is removed and additional light is available. We suspect events that create forest gaps or park-like forest stands allow *C. elata* to regenerate and colonize new sites, and the presence of hardwood trees permits populations to persist.

Implications for Conservation and Management

The habitat-related differences in plant size, fecundity, and population structure observed in this study varied among sample years, but in no cases

were plants in harvested forests smaller or less fecund than in unmanaged habitat. Rather, it appears that timber harvest in or immediately adjacent to existing *Cimicifuga elata* populations has little negative effect on plant size and fecundity, at least in the short term, and could result in population growth. Halpern and Spies (1995) showed that some forest herbs became locally extinct after forest harvest, but others persisted and increased in abundance. Even though *C. elata* occurs in small populations in a specific habitat, characteristics that may make species vulnerable to extinction after disturbance (Fischer and Stocklin 1997), it appears to respond favorably to removal of the forest canopy.

This conclusion is offered with the caveat that no information is available on the long-term viability of populations in managed forests. We could not locate any populations in second growth or plantations of moderate age (20-30 years). It may be that inventories for the species have been inadequate in this age-class (Kaye and Kirkland 1994) or competition for light and other resources excludes the species from habitats with dense tree growth. The short-term effect of timber harvest on *Cimicifuga elata* appears to be positive, but population viability in the long-term, after conifers regrow to shade the forest floor and compete for resources, could be low. In addition, clearcuts pose risks associated with disturbing the forest floor and upper soil horizons that may be harmful to some *C. elata* populations, especially on steep slopes. Therefore, clearcuts may not be the most effective means to improve conditions for the species. Habitat management techniques that retain hardwoods and lead to canopy thinning and small gaps with minimal disturbance of the forest floor may be optimal. Long-term maintenance of *Cimicifuga elata* may require that managers allow natural gap-forming processes to occur or manipulate stands to produce forest gaps that can be invaded by hardwoods. These conclusions concur with recommendations from studies of epiphytic lichens (Neitlich and McCune 1997) and forest floor bryophytes (Rambo and Muir 1998) that suggest hardwoods and small gaps promote species diversity in Northwest forests.

The positive effects of canopy disturbance on plant size may be partially off-set by increases in herbivory by deer and elk. In 1992, for example, the mean frequency of herbivory on *C. elata* in clearcuts, edges, and selectively thinned stands was two to three times greater than in unmanaged forests, second growth, and roadsides. This pattern of herbivory, in which forest openings and edges are preferred for feeding, is consistent with previous studies of the forage behavior of deer (Alverson et al. 1988, Chang et al. 1995) and elk (Schroer et al. 1993). Existing data are insufficient to measure the effect of herbivory on individual *C. elata* plant growth, so solid conclusions regarding the effect of deer and elk must await further study.

Plants on roadsides tended to be larger and more fecund than plants in old-growth forest, but roadside populations tended to have few small plants. This suggests that roadside maintenance activities, such as mowing and spraying, restrict juvenile recruitment, possibly by reducing seed production and lowering survival of small plants. Such populations might be at risk of extirpation if large plants are killed. Delaying maintenance activities until after fruit maturation (usually September) could increase seed dispersal and seedling recruitment and give these populations a more diverse structure.

Rangewide conservation of *Cimicifuga elata* populations will require a coordinated effort by various land managing agencies to maintain appropriate habitat. A Conservation Agreement between several federal agencies for this species identifies populations deemed essential for the long-term viability of the species on public lands, mandates monitoring of several populations, and prescribes conservation measures such as burning and forest density management at selected locations (USDA 1996).

Acknowledgements

We are grateful to the following individuals for help with field work: Cindy Barkhurst, Matt Carlson, Cindy Cripps, Claire Hibler, Jim Irving, Jenny Lippert, Lupin Loel, Cheshire Mayrsohn, Kathy Pendergrass, Angie Ruzicka, Larry Schofield, Alice Smith, Bryce Smith, Molly Sullivan, Julie Thiel, Molly Widmer, and Nancy Wogen. Information on population locations was provided by Washington Natural Heritage Program, Oregon Natural Heritage Program, Ruth Lewis of the Army Corps of Engineers, Ed Schreiner of Olympic National Park, and Nelsa Buckingham. Oregon State University Research

Forests generously permitted study plots on McDonald and Dunn Forests. We thank Margaret Evans, Mary Garrard, Steve Gisler, Melissa Peterson, and Jill Van Winkle for contributing their time through internships jointly sponsored by the Native Plant Society of Oregon and Oregon Department of Agriculture. Manuela Huso provided valuable statistical consulting for the loglinear analyses. Comments by John Gamon, Manuela Huso, Susan Kephart, Pat Muir, Dave Pyke, Barbara Schrader, Ed Schreiner, Alice Smith, Mark Wilson, and Nancy Wogen greatly improved this manuscript.

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Received 3 March 1999
Accepted for publication 7 June 1999

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Distribution, Abundance, and Habitat Association of Riparian-Obligate and -Associated Birds in the Oregon Coast Range

Abstract

We studied the abundance, distribution, and habitat associations of the aquatic-foraging riparian-associated vertebrate community along four stream basins transecting managed forests in the Oregon Coast Range, 1992-1994. The riparian-associated community we observed consisted primarily of birds with few observations of mammals. Belted kingfishers (*Ceryle alcyon*), American dippers (*Cinclus mexicanus*), great blue herons (*Ardea herodias*), and mallards (*Anas platyrhynchos*) comprised >85% of these observations, but we observed only one group (≥1 individual observed together) from this community for each kilometer of stream surveyed. Bird abundances among years were not different (all $P > 0.05$). Species distribution was affected by stream order, stream basin, and season in each species, but to varying degrees. Belted kingfishers, common mergansers (*Mergus merganser*), great blue herons, green herons (*Butorides striatus*), and mallards were more abundant in larger, 6th-order streams than in smaller, 4th-order streams ($P < 0.05$). Dippers used step channel units disproportionally more and riffles disproportionately less than expected ($P < 0.5$). Similarly, kingfishers used fewer riffles and more pool channel units than was expected ($P < 0.5$). Key habitat components that were predictive of use were species specific. Most notably, the presence of a forested riparian area, streamside trees, and valley walls that constrain the stream were important predictors of use by the three most abundant species; dippers, kingfishers, and great blue herons. Monitoring programs to assess populations of these species in mountainous habitat must be sensitive to the potential effects of stream order, basin, and season and encompass a large spatial and temporal extent.

Introduction

The forest lands of western Oregon and Washington are some of the most productive in the world (Franklin and Dyrness 1973, Waring and Franklin 1979). More than 78% of the approximately 35 million acres west of the crest of the Cascade Range is forested (Brown and Curtis 1985) and intensively managed for the production of wood products. Riparian areas transecting these managed forests are subject to conflicting land-use demands for development and timber harvest as well as protection for water quality and fish and wildlife habitat.

Riparian areas are important to wildlife (Bull 1978, Thomas et al. 1979, Oakley et al. 1985), but little is known about the extent of the riparian-wildlife associations in the Pacific Northwest (McGarigal and McComb 1988). Prior to 1971, timber harvest on private, state, and, to a lesser degree, federal lands proceeded without concern for riparian areas, and harvest units often have extended to the stream's edge. However, the Oregon Forest Practices Act mandated decreased harvest along streams and the retention of forested riparian areas to protect water quality and fish populations. The use by and importance of forested buffer strips to wildlife was largely unknown. In western Oregon and Washington, 87% (n = 414) of the resident species of amphibians, reptiles, birds, and mammals use riparian zones or wetlands (Oakley et al. 1985), and 10% are noted as using specialized habitats within riparian zones. In the Oregon Coast Range, most information on riparian-associated wildlife is qualitative with some quantitative information on small mammals (Anthony et al. 1987b, Corn and Bury 1991a, Suzuki 1992, McComb et al. 1993, Gomez and Anthony 1996), amphibians (Bury 1988, Corn and Bury 1991b, Gomez 1992, Vesely 1996), and songbirds (Carey 1988, Carey et al. 1991, McGarigal and McComb 1992). Even less is known about the subset of terrestrial vertebrates that are considered riparian obligates (Anthony et al. 1987a), those that depend on the stream for foraging or reproduction.

We know of no large-scale, inter-basin surveys of aquatic foraging species or assessments of factors affecting their abundance and distribution. Yet recent federal and state guidelines (e.g., FEMAT 1993, Oregon Forest Practices Act 1994) stipulate riparian reserves and require monitoring programs for selected species. Thus, the purpose of

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this study was to assess the breeding abundance, distribution, and habitat relationships of selected aquatic-foraging riparian-obligate and -associated species in the Oregon Coast Range. We evaluated habitat associations at three spatial scales (Johnson 1980) of increasing specificity: large-scale habitat patches (Johnson's 2nd level; riparian zone and streamside features; hereafter, streamside habitat); specific habitat patches (3rd level; selection among stream channel units); and selection within each patch (4th level; discrimination within each channel unit; hereafter, stream habitat). Specifically, we tested the hypotheses that: 1) the distribution and abundance of each species did not differ within and among basins, 2) species used habitat types in proportion to their availability, and 3) the stream and streamside habitat where we observed species was not different from available habitats.

Methods

Study Areas

We surveyed Drift Creek, Lobster Creek, Lake Creek, and Five Rivers basins in the central Oregon Coast Range. These basins were in Benton, Lane, and Lincoln counties and drained into the Alsea and Siuslaw rivers, 6-23 km east of the Pacific Ocean. We selected these basins arbitrarily because of logistical constraints. These basins were all in the central Coast Range and had similar elevation, gradient, vegetation, and management regimes. The topography was steep with moderately flat valleys. Stream bed elevation ranged from 3 to 365 m above sea level. Average stream gradient was generally <4% (range 0.5-5%), but was higher in smaller streams. The maritime climate was characterized by mild wet winters and cool dry summers. Average annual precipitation varied geographically and was 180-300 cm, with 75-85% falling during October-March. Mean temperature was seldom below 0°C in the winter, and summer temperatures were generally less than 27°C (Franklin and Dyrness 1973). A mosaic of federally and privately managed forests dominated the upslope areas adjacent to these streams; pastures were common along the lower portions. All basins had extensive networks of roads from past timber harvest activities, with the exception of the Drift Creek Wilderness Area. Upslope vegetation was characteristic of the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1973) dominated by Douglas–fir (*Pseudotsuga menziesii*), western hemlock, western redcedar (*Thuja plicata*), and red alder (*Alnus rubra*). Upslope seral stages ranged from recently harvested to mature forests. Riparian areas were typically forested by red alder, Douglas-fir, bigleaf maple (*Acer macrophyllum*), and western redcedar.

Stream Surveys

We surveyed the entire width (3–15 m range) of streams on foot, walking upstream (25% of surveys) or downstream (75%) within the wetted stream channel. No attempt was made to survey areas greater than 5 m from the stream edges. We surveyed portions of 5th- and 6th-order streams that were too deep to be readily walked by floating downstream in inflatable kayaks on 19 days (<12% of survey days). We conducted surveys between 0715 and 1756 hours [mean survey midpoint was 1041 hours, mean survey rate was 1.2 km / hour (n = 396)]. We excluded a 9.4-km segment of Lobster Creek and the lower 28 km of Drift Creek because of access problems.

We used the same data-collection methods during stream surveys among years but the geographic extent and the length of stream surveyed differed so that multiple research objectives could be accomplished (Loegering 1997). In May-September 1992, we used a stratified random sampling design to select stream segments to survey in the four basins. We stratified by basin and stream order, a stream classification system. Each small unbranched tributary is a first-order stream, two first-order streams join to make a second-order stream. A third-order stream is formed by the joining of two second-order streams, and so on (Strahler 1957, Everest et al. 1985). We surveyed 30 km of stream in each basin, distributed equally (10 km each) among fourth-, fifth-, and sixth-order streams. The 10 km surveyed in each order was composed of five 2-km survey units. We randomly determined the stream and location of the starting point for each survey unit in each basin and during each survey cycle. We surveyed all four basins every 3-4 weeks, completing a total of five survey cycles in 1992. In March-August 1993 and 1994, we surveyed the entire length of all 4–6th-order streams three times each year only in Drift and Lobster creek basins; Five Rivers and Lake Creek were not surveyed.

We plotted the initial locations of individuals or groups (≥1 individual in close proximity; e.g.,

an adult with a brood) of individuals of avian and mammalian species on United States Geological Survey (U.S.G.S.) 7.5' topographic maps. We plotted only observations of individuals not noticeably affected by our presence, and we made every attempt to count all individuals only once. We recorded the stream channel and streamside habitat (Appendix A) at each sighting location and at randomly-determined locations (see below) to assess habitat associations. We categorized the stream channel habitat at each location into six general units of increasing stream gradient according to Bisson et al. (1982): pools, glides, riffles, rapids, cascades, and steps (hereafter referred to as channel units). We characterized stream habitat by the channel unit length, width, and depth; channel form; streambed substrate size; number of exposed substrate items; number of pieces of large wood; and overhead vegetative shading of the stream. We used channel form to indicate if the channel contained a majority (single or primary channel) or minority (secondary or side channel) of the stream's total flow volume. We categorized the dominant substrate of stream beds into eight size classes based on particle size from smallest (=2) to largest (=9) (Platts et al. 1983).

We used six variables to characterize streamside habitat on each side of the stream; valley form, adjacent land use, riparian zone overstory vegetation, stream bank vegetation, overstory canopy cover, and the distance to human activity. We characterized the overstory riparian zone vegetation 25-m perpendicular distance from the stream at each sighting location. We visually estimated riparian zone canopy cover in a 5-m diameter plot centered 25-m perpendicular distance from the stream's edge at the sighting location. We collected data in the field and reduced it similarly for riparian zone vegetation and vegetation that was immediately adjacent to the stream (hereafter, stream bank vegetation). In the field, we visually identified the dominant plant species, defined as the species or community with the largest proportion of overstory canopy cover. For the analyses, we simplified our assessment of vegetation to one binary variable indicating if the dominant vegetation was a tree (woody vegetation > 5 m tall), or not; and a second binary variable indicating if the vegetation was a conifer, or not. Conifer trees were Douglas-fir (all size classes >5 m tall), Sitka spruce (*Picea sitchensis*), western redcedar, and western hemlock. Non-conifer trees were red alder and bigleaf maple. Young Douglas-fir (0-15 years, <5 m tall) plantations were the only vegetative category in the non–tree, conifer group. The fourth group of vegetation communities that were not trees and not conifers were shrubs, grasses, and herbs and dominated by elderberry (*Sambucus* spp.), cascara (*Rhamnus purshiana*), willow (*Salix* spp.), willow and salmonberry (*Rubus spectabilis*), salmonberry, vine maple (*Acer circinatum*), unidentified grasses or sedges, ferns or mosses, forbs, lichens, cow-parsnip (*Heracleum lanatum*), ninebark (*Physocarpus capitatus*), blackberry (*Rubus* spp.), thimbleberry (*Rubus parviflorus*), stink currant (*Ribes bracteosum*), recent clearcut with no regeneration, devil's club (*Oplopanax horridum*), skunk cabbage (*Lysichitum americanum*), stinging nettle (*Urtica dioica*), snowberry (*Symphoricarpos* spp.), horsetail (*Equisetum* spp.), salal (*Gaultheria shallon*), and red huckleberry (*Vaccinium parvifolium*). We used Hitchcock and Cronquist (1973) to identify vegetation.

Habitat Availability

We used the same stream and streamside variables to characterize the available habitat as we used to characterize used habitat in June and August, 1992. In each 2-km survey unit, we randomly sampled a minimum of 10 sites (points or locations) including at least three pools, three glides, three riffles, and all rapids and cascades, which were quite rare. The 10 sample sites were distributed uniformly along the 2-km survey unit. We used two levels of randomization in the field to reduce observer bias in selecting available channel units. Observers randomly selected 1) the type of unit to sample (e.g., pool, glide, or riffle), and 2) the direction (upstream or downstream) to travel to the next available unit of that type. These methods characterized the available channel units allowing within channel unit comparisons, but they do not represent relative abundance of these units. To determine the proportion of each available channel unit, we measured each channel unit within 500 m of each dipper nest (1000 m total) in 4–5th-order streams (>12 km total) in Drift and Lobster creeks.

Statistical Analyses

We measured stream lengths with a map wheel on 7.5' (1:24,000) U.S.G.S. topographic maps and expressed species abundance as the number of

individuals observed per km of stream. We divided all observations into early (February-June) and late (July-September) seasons to account for changes in weather patterns and hydrologic regimes in the analysis. We used similar sampling effort among basins within seasons.

We used an Analysis of Variance for an unbalanced design (ANOVA; Proc GLM, SAS Institute 1989) to compare abundances of each species in 1992 among stream basin, stream order, and survey cycle as well as all first–order interactions. We compared abundance among years with an ANOVA but limited these analyses to stream segments we surveyed all three years during comparable time periods. We used pairwise *t*-tests equivalent to Fisher's least-significant-difference (LSD) test in the case of equal cell sizes (SAS Institute 1989) for comparisons within groups. We did not examine specific effects of the survey time of day or weather because such a design was not consistent with other research objectives.

We compared the use of channel units by American dippers (*Cinclus mexicanus*) and belted kingfishers (*Ceryle alcyon*) relative to availability with a simultaneous confidence interval comparison (Bailey 1980, Cherry 1996). We defined use as the proportion of observations in each channel unit and availability as the proportion of the total area of each channel unit. We limited the analysis to 4–5th-order streams because availability data were collected only in those orders. We constructed 95% confidence intervals on use for each unit to estimate the true proportion of use. If the available proportion was less than the lower limit, channel units were used more than expected. If the available proportion was greater than the upper limit, units were used less than expected, or avoided.

We developed logistic regression models to identify stream and streamside variables that distinguished between habitats where we observed dippers, kingfishers, great blue herons (*Ardea herodias*), and mallards (*Anas platyrhynchos*) versus available habitats. Because our objective was to examine habitat selection patterns after accounting for any effects of the four stream basins, three stream orders, or two seasons, we included six indicator or dummy (0/1) variables in all regression models (3 for basin + 2 for order + 1 for season). We used a backward selection procedure to remove habitat variables that did not contribute to the regression model's explanatory power based on a drop-in-deviance test at a significance level ≤ 0.10. We compared competing models with Akaike's Information Criterion (AIC) and selected the model with the lowest score. All models met the Hosmer and Lemeshow goodness–of–fit test ($P > 0.05$, Hosmer and Lemeshow 1989). We tested all first–order interactions between significant main effects for each model after the initial variable selection. All odds ratios from logistic regression analyses are reported relative to a base comparison, that is, an odds ratio = 1. We excluded from the analysis of habitat use all observations that may have been affected by the presence of the observer, including disturbed or agitated birds, or birds in flight.

For each species, we used two models to assess habitat associations—one model compared stream habitats, and another compared adjacent, streamside habitats. Stream habitat was dynamic and may have differed among years, and we collected availability data only in 1992. Therefore, we analyzed only observations from 1992 when both use and availability data were collected. In addition, our sampling objective was to characterize the available stream habitat for each channel unit; therefore, we were limited to evaluating stream habitat selection within each channel unit (e.g., used vs. available pools). To assess streamside habitat selection, we included all observations of used habitat during 1992-1994 and the availability data collected only in 1992 because adjacent streamside features (e.g., a constrained valley form) were stable, and their availability was unlikely to change among years.

Results

We surveyed 966 km of stream (533, 230, and 203 km in 1992, 1993, and 1994; respectively) and observed 1047 groups of riparian–associated birds (96%) and mammals (<4%, Table 1).

Distribution and Abundance

Abundance was distributed differently among basins, stream orders, and survey cycle in 1992 for American dippers (ANOVA, $F = 3.3$, 52 df, $P = 0.004$), belted kingfishers ($F = 4.0$, 52 df, $P = 0.001$), common mergansers ($F = 2.5$, 52 df, $P = 0.024$), great blue herons ($F = 2.7$, 52 df, $P = 0.015$), and mallards ($F = 2.4$, 52 df, $P = 0.026$), but not for green herons ($F = 2.0$, 52 df, $P = 0.064$) or

TABLE 1. Number of groups observed and mean (SE) group size of riparian-associated species in the Oregon Coast Range, 1992-1994.

Species	Scientific name	Groups observed	% total	Group size
belted kingfisher	*Ceryle alcyon*	352	33.6	1.21 (0.03)
American dipper	*Cinclus mexicanus*	338	32.3	1.26 (0.03)
great blue heron	*Ardea herodias*	104	9.9	1.0 (0)
mallard	*Anas platyrhynchos*	101	9.6	2.94 (0.26)
wood duck	*Aix sponsa*	26	2.5	1.96 (0.39)
common merganser	*Mergus merganser*	25	2.4	5.60 (0.93)
green heron	*Butorides virescens*	21	2.0	1.05 (0.05)
unidentified ducks		17	1.6	2.18 (0.46)
hooded merganser	*Lophodytes cucullatus*	10	1.0	2.80 (0.71)
spotted sandpiper	*Actitis macularia*	4	0.4	1.25 (0.25)
domestic duck		2	0.2	5.50 (2.50)
cormorant spp.	*Phalacrocorax* spp.	2	0.2	1 (0)
other bird species[1]		5	0.5	
mammals [2]		40	3.8	
Total		1047		

[1] Other bird species includes an observation of one group each of a bald eagle (*Haliaeetus leucocephalus*), cinnamon teal (*Anas cyanoptera*), unidentified merganser, osprey (*Pandion haliaetus*), and red-breasted merganser (*Mergus serrator*).
[2] Includes 19 river otter (*Lutra canadensis*), 18 beaver (*Castor canadensis*), 2 raccoons (*Procyon lotor*), and 1 mink (*Mustela vison*).

TABLE 2. Mean (SE) abundance (individuals / 10 km of stream) of riparian-associated birds in 4–6th-order streams in the Oregon Coast Range, 1992. Values are least-squared means from the analysis of variance model including stream order, basin, and cycle effects (n = 53 surveys, 533 km of stream).

stream order	American dipper	belted kingfisher	common merganser	great blue heron	green heron	mallard	wood duck
4	2.8 (0.6) ab[1]	2.8 (0.8) a	0 (0.7) a	0.9 (0.3) a	0.1 (0.1) a	1.4 (1.2) a	0.1 (0.4) a
5	4.7 (0.6) a	7.7 (0.8) b	0.5 (0.7) a	1.2 (0.3) ab	0.4 (0.1) ab	6.0 (1.2) b	1.5 (0.4) a
6	1.4 (0.9) b	8.6 (1.0) b	4.0 (0.9) b	2.3 (0.4) b	0.6 (0.2) b	7.7 (1.6) b	0.9 (0.5) a
P	0.008	0.0001	0.002	0.015	0.029	0.005	0.082

[1]Means with the same letters within each column are not different (Fisher's LSD $P > 0.05$).

TABLE 3. Mean (SE) abundance (individuals / 10 km of stream) of riparian-associated birds in four basins in the Oregon Coast Range, 1992. Values are least-squared means from the analysis of variance model including stream order, basin, and cycle effects (n = 53 surveys, 533 km of stream).

Basin	American dipper	belted kingfisher	common merganser	great blue heron	green heron	mallard	wood duck
Drift Creek	5.7 (0.7) a[1]	5.3 (0.9) a	1.9 (0.7) a	1.2 (0.3) a	0.1 (0.2) a	1.7 (1.4) a	0.8 (0.4) a
Five Rivers	2.3 (0.8) b	6.8 (0.9) a	1.0 (0.8) a	1.5 (0.3) a	0.1 (0.2) a	5.9 (1.5) ab	0.8 (0.5) a
Lake Creek	2.6 (0.8) b	7.2 (0.9) a	0.9 (0.8) a	0.9 (0.3) a	0.6 (0.2) a	4.0 (1.5) ab	0.9 (0.5) a
Lobster Creek	1.2 (1.0) b	6.2 (1.1) a	2.1(1.0) a	2.0 (0.4) a	0.6 (0.2) a	8.5 (1.8) b	0.8(0.6) a
P	0.002	0.46	0.66	0.21	0.078	0.029	0.99

[1]Means with the same letters within each column are not different (Fisher's LSD $P > 0.05$).

wood ducks (F = 1.3, 52 df, $P = 0.27$). Dippers were more abundant in 5th than in 6th-order streams ($P < 0.05$, Table 2). Belted kingfishers, common mergansers, blue herons, and mallards were most abundant in 6th-order streams and increased monotonally from 4th to 6th-order streams ($P < 0.05$, Table 2). Dippers were more abundant in Drift Creek than the other study basins ($P < 0.05$), whereas mallards were more abundant in Lobster Creek than in Drift Creek ($P < 0.05$, Table 3). Abundance of other species did not differ among study basins. Only great blue heron

abundance differed among seasons (P = 0.01), with twice as many observations after 1 July than earlier in the year ($\bar{x}$ = 1.0, SE = 0.3 vs. $\bar{x}$= 1.9, SE = 0.2 individuals / 10 km of stream for early and late seasons, respectively). In addition, we found no significant ($P \leq 0.05$) interactions among the main effects of stream order, basin, and survey cycle for dippers, kingfishers, mergansers, great blue herons, green herons, mallards or wood ducks. There were no significant differences in abundance among years for any species (all $P >$ 0.07, Loegering 1997). In addition, we detected no autocorrelation among the years for any species (Durbin–Watson D, all $P > 0.10$).

Streamside Habitat Features

Each species was associated with different landscape and riparian zone features. Four variables distinguished areas used by American dippers from those that were available (logistic regression,χ^2 = 211, 14 df, P = 0.0001, max. re-scaled R^2 = 0.23). We located dippers in areas where trees were the dominant riparian zone overstory species on one or both stream banks (Table 4). Compared to streams with no riparian–zone trees (logistic regression odds ratio = 1), we were less likely (90% confidence interval [CI] on the odds ratio = 0.3 - 0.9, P = 0.047, Table 5) to find dippers where there were overstory trees on one side of the stream but more likely to find dippers where both banks had overstory trees. Dippers were 1.5 to 3.1 times (90% CI) more likely to be found on reaches constrained by the valley walls on both sides of the stream (P = 0.0005, Table 5) than in unconstrained stream reaches, and this pattern was similar but not as pronounced for reaches that were constrained by only one valley wall (P = 0.27). Dippers also selected areas where trees dominated the vegetation immediately adjacent to the stream on one or both sides of the stream compared to the available habitat (P = 0.64 and P = 0.06, respectively; Table 5). The interaction between stream bank trees and constrained valley form explained additional variability in the data (P = 0.06).

Three significant variables contributed to the model for habitat selection by belted kingfishers (χ^2 = 79, 11 df, P = 0.0001, max. re-scaled R^2 = 0.12). Kingfishers were 4.2 to 24 times (90% CI) more likely to use an area with trees immediately adjacent to the stream on both banks (P = 0.0001, Table 4 and Table 5) than reaches without streamside trees. However, kingfishers were only 0.5 - 0.9 and 0.4 - 0.8 times (90% CI on odds ratio) as likely to use reaches with a constrained valley form on one or both sides of the stream (both P = 0.02, Table 5) compared to unconstrained reaches (odds ratio = 1). They selected stream sections that were constrained on one or both sides less often than were available. Kingfishers also used habitat that was slightly closer to human activity (Table 4) than the available habitat (P = 0.09, Table 5).

Presence of riparian trees, the valley form, and the distance to human activity distinguished between areas used by great blue herons and those available (χ^2 = 47, 12 df, P = 0.0001, max. re-scaled R^2 = 0.11). Herons were 0.3 - 0.7 and 0.2 - 0.8 times (90% CI on odds ratio) as likely to use reaches that were constrained on one or both sides of the stream than unconstrained reaches (P = 0.007 and P = 0.03, respectively, Table 5); they used less constrained valley forms than were available (Table 4). Herons were 0.5 - 0.95 and 0.53 - 0.98 times (90%CI on odds ratio) as likely to be found where the riparian–zone vegetation was trees on one or both sides of the stream compared to treeless riparian zones (odds ratio = 1). The interaction of the distance to humans and constrained valley form also was significant (P = 0.02).

Three variables explained habitat use by mallards (χ^2 = 89, 11 df, P = 0.0001, max. re-scaled R^2 = 0.19); riparian zone canopy cover, valley form and upslope land use. Mallards were 1.3 to 4.8 times (90% CI) more likely to be found where both adjacent upslopes were managed forests (odds ratio = 2.5, P = 0.02, Table 5) rather than another land use type (odds ratio = 1). The likelihood of use by mallards decreased (odds ratio = 0.68 to 0.85, 90% CI) for each 10% increase in overstory canopy cover in the riparian area (odds ratio = 0.76, P = 0.001). Mallards also were 15% to 53% as likely (90% CI) to be located on reaches that were constrained on both sides than in unconstrained reaches (odds ratio = 0.3, P = 0.001).

Channel Unit Use and Selection. We located dippers most often in riffles (37%), rapids (27%), and pools (19%); and kingfishers were found perched over pools (47%), glides (31%), and riffles (16%). The available habitat was composed of riffles (57%), rapids (17%), glides (16%), and pools (10%). Dippers were located on steps more than expected and riffles less than expected (Table 6).

TABLE 4. Mean (SE) percent occurrence (%) and distance (m) of streamside habitat characterizing sites used by riparian-associated birds in the central Oregon Coast Range, 1992-94. * indicates variables included in the logistic regression model[1]. Samples sizes were 250,152,72,79, and 1120 for American dippers, belted kingfishers, great blue herons, mallards and the available habitat, respectively.

	Riparian Zone					Stream Bank								
	dominated by trees[2](%)		dominated by conifers[3](%)		canopy	dominated by trees[2](%)		dominated by conifers[3](%)		valley form (% constrained)		land use (% managed forests)		distance to human activity
	one bank	both banks	one bank	both banks	cover (%)	one bank	both banks	one bank	both banks	one bank	both banks	one bank	both banks	(m)
American dipper	12.8 (2.1)*	82.0 (2.4)*	30.4 (2.9)	10.4 (1.9)	52.3 (1.2)*	6.4 (1.5)*	6.0 (1.5)*	0 (0)	0 (0)	41.6 (3.1)*	33.2 (3.0)*	9.2 (1.8)	78.8 (2.6)	303 (33)
belted kingfisher	25.7 (3.5)	57.9 (4.0)	27.0 (3.6)	5.3 (1.8)	42.4 (1.8)	6.6 (2.0)*	5.3 (1.8)*	0.7 (0.7)	0.7	36.2 (3.9)*	17.1 (3.1)*	22.4 (3.4)	56.6 (4.0)	160 (29)*
great blue heron	25.0 (5.1)*	55.6(5.9)*	31.9 (5.5)	6.9 (3.0)	41.8 (2.7)	2.8 (1.9)	0 (0)	0 (0)	0 (0)	29.2 (5.4)*	20.8 (4.8)*	19.4 (4.7)	61.1 (5.7)	295 (71)*
mallard	44.3 (5.6)	41.8 (5.5)	34.2 (5.3)	6.3 (2.7)	33.5 (2.2)*	2.5 (1.8)	2.5 (1.8)	1.3 (1.3)	0 (0)	35.4 (5.4)*	15.2 (4.0)*	20.3 (4.5)*	62.0 (5.5)*	136 (32)
available habitat	30.4 (1.4)	59.3 (1.5)	25.7 (1.3)	7.1 (0.8)	43.9 (0.6)	4.5 (0.6)	0.8 (0.3)	0.2 (0.1)	0 (0)	42.4 (1.5)	18.6 (1.2)	21.6 (1.2)	60.6 (1.5)	280 (17)

[1] Species abundance and habitat features may vary among basin, stream order, and season. Presented means pool all observations whereas the statistical models assessing habitat selection first account for differences inherent to basin, stream order, and season before identifying habitat selection patterns. Consequently, the pooled means may mask more substantial differences.

[2] Contains conifer and hardwood trees.

[3] Contains conifer trees and shrubs.

TABLE 5. Variables distinguishing between used and available streamside habitat for American dippers, belted kingfishers, great blue herons, and mallards in the Oregon Coast Range, 1992-1994. Wald χ^2 and P values are from logistic regression models fitted with indicator variables for basin, stream order, and season. Each set of variables remained after backward logistic regression eliminated others at a significance level = 0.10. See Loegering (1997) for model details.

Species Habitat variable	Wald's χ^2	P	Odds ratio[1]	90% confidence interval on odds ratio Lower	 Upper
American dipper					
tree-dominated riparian zone (%)					
- one bank	3.9	0.047	0.47	0.3	0.9
- both banks	0.6	0.431	1.35	0.7	2.5
riparian zone canopy cover (10% increments)	2.3	0.131	1.08	1.0	1.2
trees on the stream bank (%)					
- one bank	0.2	0.642	1.23	0.6	2.6
- both banks	3.6	0.058	3.52	1.2	10.5
constrained valley form					
- one bank	1.2	0.273	1.23	0.9	1.7
- both banks	12.3	0.001	2.15	1.5	3.1
streambank trees * constrained valley form	3.6	0.059	1.68	1.1	2.6
belted kingfisher					
trees on the stream bank (%)					
- one bank	2.2	0.135	1.76	0.9	3.3
- both banks	18.6	0.000	10.07	4.2	24.3
constrained valley form					
- one bank	5.2	0.022	0.63	0.5	0.9
- both banks	5.4	0.020	0.54	0.3	0.8
distance to human activity (km)	2.8	0.095	0.62	0.4	1.0
great blue heron					
tree-dominated riparian zone (%)					
- one bank	3.2	0.075	0.49	0.3	0.9
- both banks	2.9	0.088	0.53	0.3	1.0
constrained valley form					
- one bank	7.4	0.007	0.44	0.3	0.7
- both banks	4.5	0.033	0.42	0.2	0.8
distance to human activity (km)	1.5	0.220	0.52	0.2	1.2
distance to humans * constrained valley form	5.6	0.018	2.23	1.3	3.9
mallard					
riparian zone canopy cover (10% increments)	15.1	0.000	0.76	0.7	0.9
constrained valley form					
- one bank	2.3	0.126	0.65	0.4	1.0
- both banks	10.6	0.001	0.28	0.1	0.5
upslopes managed forests					
- one bank	0.1	0.751	1.14	0.6	2.3
- both banks	5.6	0.018	2.53	1.3	4.8

[1] multiplicative likelihood of use given a 1-unit increase in the value of a given variable. Odds <1 indicate that an increase in the value of that variable decreases the likelihood of use whereas odds >1 indicate a greater likelihood of use with an incremental increase in the value of that variable.

TABLE 6. Channel unit use by American dippers (n = 95) and belted kingfishers (n = 32) in Drift and Lobster creeks in the Oregon Coast Range, 1992-1994. Proportion of available habitat calculated from the area of 269 channel units (total length = 12,273 m, total area = 91,047 m^2).

Channel unit	Number of observations	Proportion[1] of available channel units	Proportion of observed use	95% confidence limit on observed use		Selection[2]
				Lower	Upper	
American dipper						
pool	18	0.098	0.189	0.093	0.311	0
glide	7	0.162	0.074	0.018	0.169	0
riffle	35	0.569	0.368	0.237	0.503	-
rapid	26	0.167	0.274	0.158	0.404	0
cascade	3	0.003	0.032	0.001	0.110	0
step	6	0.000	0.063	0.013	0.155	+
Total	95	100	100			
belted kingfisher						
beaver pond	1		0.031	0.004	0.198	
pool	15	0.098	0.469	0.231	0.689	+
glide	10	0.162	0.313	0.116	0.542	0
riffle	5	0.569	0.156	0.027	0.370	-
rapid	1	0.167	0.031	0.004	0.198	0
cascade	0	0.003				
step	0	0.000				
Total	32	100	100			

[1] Proportion of channel units represents expected bird observations if each habitat was used in exact proportion to availability.
[2] Channel units used less than (-), more than (+), or in proportion (0) to expected use with the assumption of proportional use.

Kingfishers were found over pools more than expected and riffles less than expected (Table 6). No other species had adequate sample sizes to assess selection of channel units.

Stream Habitat Features

Pool channel units were different between used and available habitat for dippers ($\chi^2 = 45$, 9 df, $P = 0.0001$), kingfishers ($\chi^2 = 35$, 7 df, $P = 0.0001$), herons ($\chi^2 = 25$, 8 df, $P = 0.002$), and mallards ($\chi^2 = 24$, 8 df, $P = 0.002$). Pools used by dippers were more likely to be shorter (Table 7, odds ratio = 0.97, $P = 0.06$), wider (odds ratio = 1.1, $P = 0.04$), and had larger substrate items (odds ratio = 1.4, $P = 0.06$, Table 8) than the available pools (odds ratio = 1). Great blue herons and mallards selected pools that were more open and were in secondary channels. Both species were observed in secondary channel pools 11% and 8% of the time even though these pools comprised only 2% of the available habitat. Consequently, stream segments with pools adjacent to the primary channel increased the likelihood of use by herons and mallards by 3 to 34 and 1.4 to 19 times (90% CI; odds ratios = 9.7 and 5.2; $P = 0.003$ and $P = 0.04$, respectively). Herons and mallards used shaded stream segments less than available. A 10% increase in stream shading decreased the likelihood of use by approximately 23% and 20% for herons and mallards ($P = 0.002$, and $P = 0.03$, respectively; Table 8).

Glide channel units used by kingfishers were different than available glides ($\chi^2 = 24$, 9 df, $P = 0.005$; Table 8). The likelihood that a kingfisher would use a glide increased with glide length (odds ratio = 1.02, $P = 0.07$). However, the likelihood of kingfisher use decreased with increasing substrate size class (odds ratio = 0.8, $P = 0.06$) and the number of exposed substrate items (odds ratio = 0.97, $P = 0.09$).

Riffle use by dippers and kingfishers differed than availability ($\chi^2 = 24$, 7 df, $P = 0.001$ and $\chi^2 = 18$, 8 df, $P = 0.025$; respectively). The likelihood of dipper use decreased with an increase in the number of pieces of large wood in the riffle (odds ratio = 0.94, $P = 0.08$) compared to the available habitat (odds ratio = 1). Kingfishers used riffles that were longer (odds ratio = 1.05, $P = 0.04$) and deeper (odds ratio = 1.1, $P = 0.003$) than the average riffle (odds ratio = 1).

TABLE 7. Mean (SE) stream habitat characterizing sites used by riparian-associated birds in the Oregon Coast Range, 1992. * indicates variables included in the logistic regression model[1]. Loegering (1997) contains a more detailed summary.

Channel unit / Species	n	Channel unit dimensions: Length (m)	Width (m)	Depth (cm)	Channel form[2]	Substrate size[3]	Exposed substrate (#/100 m²)	Large wood (#/100 m²)	Stream shading (%)
Pool									
American dipper	21	19.1 (3.7)*	9.9 (1.1)*	40.0 (4.2)	4.8 (4.7)	7.5 (0.2)*	11.9 (3.4)	2.4 (1.4)	37.4 (5.6)
belted kingfisher	60	109 (32.1)	14.0 (0.8)	59.0 (6.9)	1.7 (1.7)	7.0 (0.3)	2.5 (0.7)	0.8 (0.2)*	23.3 (3.2)
great blue heron	37	123 (44.8)	11.1 (1.1)	63.0 (9.6)	10.8 (5.1)*	6.4 (0.3)	3.2 (1.2)	2.4 (0.6)	21.2 (3.6)*
mallard	37	76.3 (27.9)	13.7 (1.1)	56.3 (6.8)	8.1 (4.5)*	6.5 (0.4)	4.7 (3.2)	0.7 (0.2)	19.4 (3.0)*
available habitat	342	76.0 (9.7)	11.0 (0.4)	56.6 (2.2)	2.05 (0.8)	6.5 (0.1)	8.2 (2.0)	4.5 (1.0)	32.5 (1.4)
Glide									
American dipper	28	13.5 (1.5)	7.4 (0.9)	25.0 (1.8)	3.6 (3.5)	7.6 (0.2)	20.1 (4.5)	2.2 (1.2)	44.6 (5.2)
belted kingfisher	33	24.9 (5.9)*	10.9 (1.1)	27.6 (2.9)	0 (0)	7.4 (0.3)*	4.7 (1.5)*	1.1 (0.3)	27.9 (4.2)
great blue heron	11	13.9 (2.7)	11.1 (1.6)	25.9 (2.0)	0 (0)	7.6 (0.6)	9.5 (3.5)	2.0 (1.2)	29.0 (9.4)
mallard	17	17.3 (2.0)	11.5 (1.5)	30.0 (4.0)	0 (0)	8.1 (0.3)	3.9 (1.8)	1.4 (0.6)	21.5 (3.4)
available habitat	337	15 (0.7)	8.3 (0.3)	25.5 (0.7)	0 (0)	7.5 (0.1)	30.9 (5.0)	4.4 (0.7)	37.2 (1.5)
Riffle									
American dipper	59	14.8 (1.4)	6.4 (0.6)	16.1 (1.2)	1.7 (1.7)	7.5 (0.1)	63.2 (16.4)	1.4 (0.3)*	43.2 (3.9)
belted kingfisher	14	20.7 (3.7)*	8.8 (1.6)	22.9 (4.0)*	0 (0)	7.4 (0.3)	57.3 (41.0)	0.7 (0.5)	34.7 (9.1)
great blue heron	4	21.7 (8.2)	9.6 (2.7)	21.3 (5.9)	0 (0)	6.5 (1.0)	7.9 (4.2)	52.1 (52.1)	18.8 (10.3)
mallard	4	15.9 (3.7)	15.4 (4.0)	21.3 (5.2)	0 (0)	8.5 (0.5)	12.1 (3.3)	0 (0)	10.0 (3.5)
available habitat	344	14.2 (0.6)	8.0 (0.3)	16.5 (0.5)	1.5 (0.6)	7.6 (0.1)	57.3 (5.2)	6.7 (2.3)	36.9 (1.5)
Rapid									
American dipper	12	6.3 (2.1)	6.5 (1.3)	16.7 (3.4)	0 (0)	8.0 (0.3)	68.6 (17.9)	2.6 (1.3)	42.9 (9.3)
available habitat	45	8.5 (1.1)	10.0 (1.0)	22.1 (1.7)	0 (0)	8.4 (0.1)	37.9 (8.5)	2.0 (0.7)	26.5 (4.4)
Cascade									
American dipper	3	20.0 (15.0)	13.2 (4.6)	35.0 (7.6)	0 (0)	8.3 (0.3)	25.4 (11.4)	1.0 (0.6)	63.3 (8.8)
available habitat	11	11.5 (3.0)	11.1 (1.5)	16.8 (2.5)	9.1 (8.7)	8.4 (0.2)	18.9 (5.4)	0.6 (0.4)	45.9 (9.4)
Step									
American dipper	6	2.1 (1.2)	6.6 (2.5)	28.3 (13.3)	0 (0)	8.2 (0.4)	75.1 (40.8)	20.1 (13.2)	44.2 (11.4)
available habitat	19	3.8 (1.6)	7.8 (1.2)	15.6 (3.8)	0 (0)	8.9 (0.1)	107.0 (45.6)	99.7 (90.4)	40.7 (6.3)

[1] Species abundance and habitat features may vary among basin, stream order and season. Presented means pool all observations whereas the statistical models assessing habitat selection first account for differences inherent to basin, stream order, and season before identifying habitat selection patterns. Consequently, the pooled means may mask more substantial differences.

[2] Percent of locations in the secondary channel.

[3] Size class of the average substrate particle from the smallest (clay = 2) to largest (bedrock = 9, Appendix A).

Discussion

Distribution and Abundance

All riparian–associated birds we studied differed in abundance and distribution among stream basins and stream orders. Factors explaining these differences include differences in the response of these species to basin and stream order differences in geomorphology, topography, hydrology, and riparian zone vegetation (Loegering 1997). Differences in abundance among basins likely reflected the differences in the geomorphology of those basins. Only dippers were more abundant in Drift Creek than in other basins, Drift Creek was the highest–gradient basin, and dippers typically inhabit swift mountain streams (Kingery 1996). Mallards were more abundant in Lobster Creek than in other basins, and Lobster Creek was a low–gradient stream with many pools and slow–water channel units. The juxtaposition of grass–dominated agricultural lands and these low-gradient streams in Lobster Creek may be important for mallard brood rearing because most of the groups we observed were adult females with young. Regardless of the underlying geomorphic and management differences among the four basins, kingfishers were similarly abundant

TABLE 8. Variables distinguishing between used and available stream channel units for American dippers, belted kingfishers, great blue herons, and mallards in the Oregon Coast Range, 1992. Wald χ^2 and *P* values are from logistic regression models fitted with indicator variables for basin, stream order, and season. Each set of variables remained after backward logistic regression eliminated others at a significance level = 0.10. See Loegering (1997) for model details.

Species Variable	Wald's χ^2	*P*	Odds ratio[1]	90% confidence interval on odds ratio Lower	 Upper
American dipper					
Pool					
Length	3.5	0.063	1.0	0.9	1.0
Width	4.2	0.041	1.1	1.0	1.2
Substrate Size	3.6	0.057	1.4	1.0	1.8
Riffle					
Pieces of wood / 100 m2	3.0	0.083	0.9	0.9	1.0
belted kingfisher					
Pool					
Wood / 100 m2	2.2	0.141	0.9	0.8	1.0
Glide					
Length	3.1	0.074	1.0	1.0	1.0
Substrate Size	3.7	0.056	0.8	0.6	1.0
Exposed rocks / 100 m2	2.9	0.091	1.0	0.9	1.0
Riffle					
Length	4.14	0.042	1.05	1.0	1.1
Depth	8.84	0.003	1.10	1.0	1.2
great blue heron					
Pool					
Shade (10% increments)	10.0	0.002	0.8	0.7	0.9
Secondary Channels	8.9	0.003	9.7	2.8	33.9
mallard					
Pool					
Shade (10% increments)	4.9	0.027	0.8	0.7	0.9
Secondary Channels	4.3	0.039	5.2	1.4	19.3

[1] Multiplicative likelihood of use given a 1-unit increase in the value of a given variable. Odds <1 indicate that an increase in the value of that variable decreases the likelihood of use whereas odds >1 indicate a greater likelihood of use with an incremental increase in the value of that variable.

throughout the study area. However, kingfisher abundance may have been ameliorated because they will readily use a number of different substrates for nesting burrows (Hamas 1994). These include road cuts (Bent 1940) along the extensively–roaded study area, as well as cut–banks along the stream (Davis 1982) and banks created by headwall failures (pers. obs.). In addition, they can range a great distance from nest sites and may nest up to 2.4 km from the water (Hamas 1974, Prose 1985).

The abundance of riparian–associated species differed by stream order and likely reflects the ecology and behavior of the birds we observed. Mallards and mergansers often used streams as loafing and brood–rearing habitat, and their abundance was greatest lower in the basins. Both the frequency and extent of micro–habitats with lower stream velocities was greater here, allowing birds to expend minimal energy to maintain position. However, most dippers, kingfishers, and herons we observed were actively foraging and their abundance likely reflected their selection of foraging habitat. Dipper associations with streams <15 m wide and nest sites on stream-side cliffs (Kingery 1996, Loegering 1997) likely limited dipper distribution to the lower order, higher gradient, streams. Similarly, herons found more suitable foraging micro–habitat, such as slow-moving, off–channel pools (e.g., Butler 1992), in the larger streams lower in the basins.

Riparian-associated birds in the Oregon Coast Range were generally less abundant than elsewhere in North America. Dippers were over 4

times more abundant in Montana and Colorado. Sullivan (1973) and Price and Bock (1983) report breeding densities >1.0 *nests* / km and Ealey (1977) observed 1.2 *birds* / km compared to 0.2–0.5 *birds* / km in our study. The 5th-order reach of Drift Creek, with the most abundant dipper population, was marginally comparable ($\bar{x} = 0.97$ birds / km, SE = 0.13, n = 12 surveys). Parsons (1975) found 1-4 dippers / km during the winter in the Oregon Cascades. The breeding density of Eurasian dippers (*C. cinclus*) in Europe averaged >1 adult / km (Ormerod et al. 1985, Daulne 1990, Vickery 1991). Availability of nest sites may have limited the overall abundance of dippers in our study area (Loegering 1997) as has been concluded elsewhere (Price and Bock 1983, Fite 1984, Kingery 1996). Streams where we saw dippers often had nests nearby. However, we rarely saw dippers in streams that contained no suitable nest sites, regardless of the apparent ecological similarity to streams where dippers where present.

Abundance of kingfishers in fifth and sixth-order streams was nearly 1 individual / km of stream, whereas all other species were less than half that abundance. Breeding densities in similar sized streams in Pennsylvania were comparable (Brooks and Davis 1987); however, in Ohio, breeding densities were nearly four times larger (Davis 1982). Studies of kingfishers in mountainous habitat are few.

Overall, we saw slightly more than one group of riparian–associated species for each kilometer of stream surveyed but no single species was very abundant. Although we believe there is no alternative way to sample this community, future research must expect the labor-intensive nature of these studies. Also, abundance estimates may have been biased because of different probabilities of detecting and identifying each species. This bias may have been greatest in stream sections with difficult footing where the observer split attention between looking ahead and carefully placing nearly every step. Although we did not directly quantify this bias, we offer this assessment. Dippers were likely censused. They seldom leave the course of the stream (Kingery 1996), and did not avoid human contact. Kingfishers and herons, however, occasionally left the area quietly and some birds may have been missed by an observer. Moreover, the low incidence of mammals in our study likely reflects the bias of our daytime surveys and not the relative abundance of these species.

Streamside Habitat Association

Selection of streamside habitat by dippers, kingfishers, herons, and mallards was disproportional to availability, and the valley form was the only factor important to all four species. Dippers were associated with streams having riparian zones and stream banks dominated by trees on both sides. This was especially important because dippers were more abundant in the smaller, high gradient streams, where forests managed for timber production were common in the Oregon Coast Range. Constrained valley forms also were important predictors of dipper use, a likely correlate of their affinity to mountain streams (Kingery 1996).

Kingfisher's association with streamside habitat in less constrained reaches and the presence of stream-side trees are a consequence of its foraging ecology. Kingfishers were associated with the presence of trees on the stream banks, yet these features occurred <7% of the time. Presumably trees on the stream bank provide perches from which kingfishers detect prey; most of the perched birds we observed were on the branches of streamside trees. Moreover, kingfishers are generally absent from habitats lacking perches (Hamas 1994, Root 1988). Kingfishers may be simply responding to salmonid abundances when selecting to forage in less constrained stream reaches. In the Oregon Cascades, cutthroat (*Oncorhynchus clarki*) and rainbow (*O. mykiss*) trout abundance in unconstrained reaches was more than double than in adjacent constrained reaches (Moore and Gregory 1989). Great blue herons also may be responding to prey abundances as they selected stream reaches in less constrained valleys.

Dippers, kingfishers, and mallards were associated in some way with a tree–dominated riparian zone; however, the minimum or optimum riparian buffer strip that is needed for these species is unclear. We did not evaluate different widths of riparian buffer strips but limited our evaluation of the riparian forest to a single plot 25 meters from the stream at each point a bird was located. Current forest practices rules protecting riparian areas generally meet or exceed this distance on federal land, but not on private lands. Riparian reserves on federal lands require limited or no harvest within 91 m (300') of fish-bearing streams (FEMAT 1993). In contrast, Oregon Forest Practices Rules call for riparian management areas with requirements to retain targeted stocking levels

within 30 m (100') of the stream on state and private lands. The extent that these stocking levels adequately provide habitat for riparian-associated species remains unclear. Many vertebrates, especially riparian mammals, reptiles, and amphibians, are active within 60 m of water (Brinson et al. 1981). Consequently, establishing the appropriate buffer-strip width must consider factors such as the target species or community, location within the stream basin, and the composition of the current riparian zone. Harvest of stream-side trees has been commonplace and many streams have little or no legacy of large trees that can contribute large wood to the stream. Minimum conifer stocking levels (Oregon Forest Practices Act 1994) developed to retain and recruit large wood may change the composition of hardwood-dominated riparian areas in the Coast Range. Fortunately, dippers, kingfishers, and great blue herons appear to respond to the riparian forest structure and not whether the forest is coniferous or deciduous.

Channel Unit Selection

Dippers and kingfishers were found along the same streams; however, they selected different channel units early in the breeding season. Although we found dippers less often than expected in riffle units, it is important to note that these units represent >30% of observed use and >56% of the available habitat. While they may use disproportionately fewer riffles, dippers were observed foraging nearly one-third of the time in riffles (unpubl. data) and riffles may provide important foraging habitat during other time periods (e.g., brood-rearing; Loegering 1997).

Kingfishers strongly selected pools and avoided riffles in this study. Conversely, foraging kingfishers selected riffles, rather than pools in Pennsylvania and Ohio (Davis 1982, Brooks and Davis 1987); specifically, the downstream tail-out transition to pools within riffles were selected (Brooks and Davis 1987). Although seemingly contradictory, these observations are consistent in that the kingfishers were responding to fish distributions. Brooks and Davis (1987) observed fish abundance was greatest in the downstream portion of riffles, and we believe their study streams may have been lower gradient than those in our study. Hamas (1994) hypothesized that "fast currents that reduce visibility" may reduce foraging effectiveness. Most of our observations were of birds perched over the stream and presumably foraging. The fourth- and fifth-order streams we evaluated were high gradient (1-3%) with higher surface turbulence and visual disturbance than in Pennsylvania or Ohio. Moreover, salmonids, primarily juvenile coho salmon (*Oncorhynchus kisutch*), were more abundant in pools (Phillips 1986, Bisson et al. 1988, Schlosser 1991).

Stream Habitat Association

Channel unit length, width, and depth, secondary channels, wood, substrate size, exposed substrate items, and stream shading were useful in discriminating between pools, glides, and riffles that were used versus those available; however, many confidence intervals on the odds ratio indicated marginal statistical significance and low statistical power (i.e., spanning or approaching 1.0). Channel heterogeneity and structural complexity were important features. Pools that were in a secondary or side channel with less shade were more likely to be used by mallards and great blue herons. Generally, these pools had sustained flow during the winter months when stream flow was highest. However, as flow volume decreases throughout the summer, the pools were partially or entirely cut off from the main channel, trapping prey or creating a current-free loafing site.

Belted kingfishers strongly selected sites with trees on both stream banks, and they were located above pools more than expected based on channel unit availability. However, kingfishers were less likely to use pools with more wood in them. This paradox may be the result of historical harvest extending to the stream, thereby eliminating recruitment of large wood during the past two decades. Alternatively, the increase in channel unit complexity because of wood may reduce kingfisher foraging efficiency (e.g., Kelly 1996) and high complexity units would be used less frequently. In addition, kingfishers were located above riffles less frequently than expected, but the likelihood of finding them over a riffle increased with increasing stream depth.

Finally, we recognize a number of limitations of this study. We chose the four study basins subjectively, representing a non-random sample of the Oregon Coast Range. Consequently, inference of abundance to larger geographic scales beyond these basins should be done with caution. Although

several important habitat variables were identified by the logistic regression models, none explained >25% of the observed variability (R^2). Although the variables identified by the habitat selection models contributed to the model's fit and as a whole were important descriptors of the habitat–use patterns we observed, they individually were not different from a zero effect (i.e., 90% CI on the odds ratio included or approached 1.0). In part, this may be attributed to the natural variability in the environment, variable habitat selection patterns for each species, and variability among the stream orders and basins we studied. Further improvement of sampling techniques, habitat quantification, and focusing on a more specific spatial and temporal scale may improve the study's explanatory power but also may decrease the generality.

Management Implications

Because these systems are intensively managed for forest products, we offer these suggestions. Managers should consider the basic ecological information on species composition, abundance, and habitat associations of riparian-associated species, including terrestrial riparian-associated species not addressed by this study, when refining the goals and objectives of riparian zone management. Monitoring programs to assess populations of these species must be sensitive to the potential effects of stream order, basin, and season. The low abundance and sparse distribution of these species in the Oregon Coast Range provide additional challenges in evaluating the cumulative effects of management within and among basins. Population–level responses may be difficult to quantify at the scale of most silvicultural experiments (e.g., 200-m long riparian management zones). Monitoring plans and riparian zone management attempts should consider a large spatial (e.g., watersheds) and temporal extent to detect species presence and account for differences in abundance among basin and order. Monitoring at smaller spatial scales could be inadequate and allow cumulative impacts on the entire watershed to go undetected. We strongly recommend an *a priori* assessment of study objectives and statistical power to evaluate the potential success of the project.

Trees on the bank immediately adjacent to the stream were associated with increasing likelihood of use by dippers and kingfishers, the two most abundant species. Management regimes and silvicultural prescriptions should retain or establish streamside trees. Riparian zones dominated by tree species were positively associated with dippers, and were present at 95% of our dipper observations. However, appropriate riparian buffer strip widths need to be evaluated at a variety of spatial scales.

Few attributes were different between used and available channel units, and most significant variables would be difficult to successfully manage (e.g., substrate size). Riparian zone management should include aspects that maintain stream channel heterogeneity, allow the stream to interact with the flood plain, and include secondary and alternate channels within the riparian forest. Policies that encourage channel heterogeneity and retain large wood also would benefit riparian-associated species by providing varied habitats, although kingfishers were negatively associated with wood in pools.

Wildlife associated with riparian areas are important resources. As riparian areas become more intensively managed, the challenge will be to create strategies that do not compromise the ecological requirements of riparian-associated species. Efforts to monitor and maintain stream systems with good water quality and sustainable populations of aquatic invertebrates and vertebrates should protect the resources needed by riparian obligates. Conservation strategies developed for terrestrial riparian wildlife, fish, and aquatic habitat (e.g., Bisson et al. 1992, FEMAT 1993, Thomas et al. 1993:427-482) that focus on the restoration and maintenance of physical and biological integrity of aquatic systems (Karr et al. 1986, Karr 1991, Naiman et al. 1992) should protect riparian-associated species as well.

Acknowledgements

The Coastal Oregon Productivity Enhancement Program and the Bureau of Land Management funded this study. The Oregon Cooperative Wildlife Research Unit provided financial and technical support throughout the entire project. We are grateful to N. Verne Marr, Lisa Loegering, Ken Popper, Amy Deller, Jennifer Purvine, and Julie Rosenthal for field assistance. Catherine Ortega and one anonymous reviewer provided comments that improved the manuscript.

Appendix A.

Habitat variables assessed at bird locations and randomly-selected points along Oregon Coast Range streams, 1992-1994.

Variable	Units
Stream habitat	
channel unit	pool, glide, riffle, rapid, cascade, step (from Bisson et al. 1982)
length, width, and depth	meters
channel form	single or primary vs. secondary, tertiary, or side channel
substrate size	8 size classes based on particle size: clay (<0.004 mm), silt (0.004-0.062 mm), sand (0.062-2 mm), small gravel (2-32 mm), large gravel (32-64 mm), cobble (64-500 mm), bolder (500-2000 mm), and bedrock (>2000 mm) (Platts et al. 1983)
exposed substrate	number / m^2 of exposed rocks <0.25 m high and surrounded by water in the channel unit
wood	number / m^2 of pieces >1 m long and 0.3 m diameter in the channel unit
shade	% of stream shaded from directly above by vegetation
Streamside habitat	
valley form	unconstrained or constrained (valley floor < twice the active channel width)
adjacent land use	managed forests or not
riparian zone[1] vegetation and stream bank vegetation	Dominant species at each location reduced to 2 indicator variables for 1) the presence of trees taller than 5 m versus shrubs, grasses, or herbaceous plants and 2) whether the vegetation was coniferous or not
riparian zone[1] canopy cover	% canopy cover of adjacent forest overstory visually estimated in a 5-m diameter plot 25 m from the stream
human activity	distance (m) to nearest area frequented by humans (e.g., roads, dwellings, etc.)

[1] Evaluated 25-m perpendicular distance from the stream bank.

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Received 6 October 1998
Accepted for publication 28 April 1999

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Wetland Development in Primary and Secondary Successional Substrates Fourteen Years after the Eruption of Mount St. Helens, Washington, USA

Abstract

The eruption of Mount St. Helens deposited new substrates upon which wetlands are now developing. Furthermore, the blast damaged vegetation in wetlands surrounding the deposition area. This study describes wetlands in the blast zone north of the crater as documented 14 years after the 1980 eruption with 220 100 m^2 plots. Five wetland types were recognized in the field: moist areas, wet areas with shallow standing water, seasonal streams, permanent streams, and ponds or lakes. The variables, elevation, slope and aspect were determined; hot water springs were discriminated from cold water springs by a nominal variable, and substrate was characterized as stable or unstable. Four levels of disturbance intensity were recognized. Spatial variables, i.e., the position of wetlands on the landscape, were also used in analysis of the data.

Using TWINSPAN, we organized the vegetation into 24 wetland plant communities. Based on canonical correspondence analysis, we determined that the measured environmental and spatial variables were unimportant in structuring primary successional vegetation. The lack of a relationship between the wetland types and environmental factors in the primary successional wetland communities suggests that stochastic events, such as seed dispersal, have played a leading role in early primary succession. Vegetation within secondary successional wetlands appears to be more closely related to the wetland types and environmental variables. Thus we conclude that environmental factors were more important in structuring wetland vegetation in areas that were less impacted by the eruption than in those areas where wetlands were newly created.

Introduction

The massive 1980 lateral eruption of Mount St. Helens, Washington, destroyed, altered and created many wetland areas. New wetlands were formed in depressions within the volcanic substrates. The blast damaged vegetation in existing wetlands and blanketed vast areas with air-borne tephra. This study documents the plant communities of the many wetlands found in the blast zone north of the crater. These wetlands range from newly formed wetlands to those that were only slightly altered by the eruption. Thus, a gamut of recovery patterns occur and are analogous to those described by Grishin et al. (1996) in Kamchatka, in that primary succession, secondary succession and simple recovery from damage were documented.

Colonization by vegetation in any newly formed wetland requires successful dispersal and establishment. The chance that a propagule will reach an isolated site is low, and is constrained by distance to a source (del Moral and Wood 1993a), weather (Walton 1990, Titus and del Moral 1998), and seed dispersal ability (Stöcklin and Bäumler 1996). The chance that the propagule will lodge in a favorable microsite is determined by surface features (Tsuyuzaki and Titus 1996), the availability of nutrients and water (Stöcklin and Bäumler 1996), and other physical and biological factors. The joint probability that a propagule arrives in a suitable site at the right time must, for isolated sites, be extremely low (Walton 1990), though it increases through time. Consequently, primary succession in isolated areas can be considered strongly stochastic, i.e., subject to random events (Talling 1951, Margalef 1963, del Moral 1993), and this stochasticity may, in part, determine eventual vegetation patterns over large scales (Collins and Glenn 1990, 1991, Collins et al. 1993). In new, barren areas on Mount St. Helens, wet sites were the first to be colonized (del Moral and Wood 1986). The first immigrants were small-seeded species with high dispersal ability (e.g., *Salix* spp., *Epilobium* spp.) or spore-producing species (e.g., *Equisetum*, mosses) (del Moral and Bliss 1993).

We predict that, in early primary succession, environmental stress coupled with a limited potential colonization pool prevents a significant

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correlation between species composition and environmental factors (Chesson and Case 1986, Davey and Rothery 1993). Alternatively, site-specific conditions could strongly influence early species composition in a consistent way (Tsuyuzaki 1997). In recovering wetlands, i.e., secondary successional, the long history of competitive rearrangement and opportunity for most available species to colonize implies that environmental conditions will constrain community composition and lead to predictable species assemblages. Thus, we hypothesize that secondary successional wetlands are more highly correlated with environmental factors than are primary successional wetlands. This study assesses the vegetation of early successional wetland communities that have assembled within the blast zone of Mount St. Helens, the relationship between these and more developed wetland communities, and the influence of environmental, spatial and stochastic factors on the vegetation.

Methods

Study Area

The lateral eruption of May 18, 1980, created a wide range of disturbance around Mount St. Helens (46°12' N, 122°11' W). The main force of the eruption was directed northwards, hence this study focuses on wetlands in the blast zone north of the crater, much of which is encompassed by the Pumice Plain and the Margaret Range (Figure 1).

The study area climate is maritime with cool, wet winters and warm, dry summers (del Moral and Bliss 1993). Information collected by the former Spirit Lake Ranger Station indicates that annual precipitation fluctuates greatly about a mean of 237 cm, drought is common during July and August, and mean temperatures range from a -4° C minimum to a 0°C maximum in January and a minimum of 7°C and a maximum of 22°C in August (Spirit Lake Ranger Station [987 m a.s.l.], Pacific Northwest River Basins Commission 1969).

Pumice was deposited over the entire study area in depths ranging from hundreds of meters near the cone to tens of centimeters at the edge of the blast zone. Where significant depositions of pumice accumulated, the resulting pumice soils are immature and extremely nutrient poor and contain very low concentrations of carbon and nitrogen (Nuhn 1987, del Moral and Bliss 1993, Titus unpubl. data).

A wide variety of wetland communities with varying levels of damage from the eruption occur within the study area. The crater, 1750-2000 m a.s.l., has several vegetated seeps in stable areas, but streams in the crater are unstable and support no vegetation. Fumeroles on the lava dome create hydric substrates where the steam condenses; these unstable substrates are infrequently vegetated (one plot only in this study). The Pumice Plain, 1150 to 1300 m a.s.l., covers 20 km^2 north of the cone and was formed by the debris avalanche, pyroclastic pumice flows, tephra deposits and later mudflows (Foxworthy and Hill 1982). Pumice Plain vegetation was described by del Moral et al. (1995) and Titus et al. (1998). Streams that dissect the Pumice Plain are either permanent or seasonal, the latter of which flows only during snowmelt. The stability of streambanks varies widely depending upon the stability of upstream tephra deposits. Many cold water springs and occasional hot water springs occur on the Pumice Plain, primarily near the north shore of Spirit Lake. The largest wetlands also occur near Spirit Lake in this same area.

Spirit Lake, 1300 m a.s.l., located north of the Pumice Plain, reformed on new substrates after the eruption. Due to fears of floods along the Toutle Valley, the lake level was lowered in 1983 via a constructed tunnel. Wetlands then formed on the newly exposed surfaces along the south shore of the lake; the other shores of the lake are very steep.

On steep north-facing slopes located near the Pumice Plain and Spirit Lake, areas that were heavily impacted by the blast were covered by snow and faced away from the eruption. These areas provided refuge for many species and enabled them to survive the eruption as rootstock, particularly late-successional forest understory species (Titus et al. 1998). After the eruption, erosion quickly removed the pumice layer and exposed rootstock was able to resprout. Refugia wetlands include riparian wetlands in the Margaret Range, wetlands along Cedar Creek, Smith Creek and other creeks that flow from Windy Ridge, sporadic wetlands along Green River, and wetlands on the east side of the Pumice Plain (Figure 1).

Further from the cone, some vegetation survived at Meta Lake (1103 m elevation, 18 km north of the crater), Ryan Lake (1080 m elevation, 26 km north of the crater), and St. Charles Lake (1262 m elevation, 17 km north of the crater). These lakes have shoreline wetland vegetation

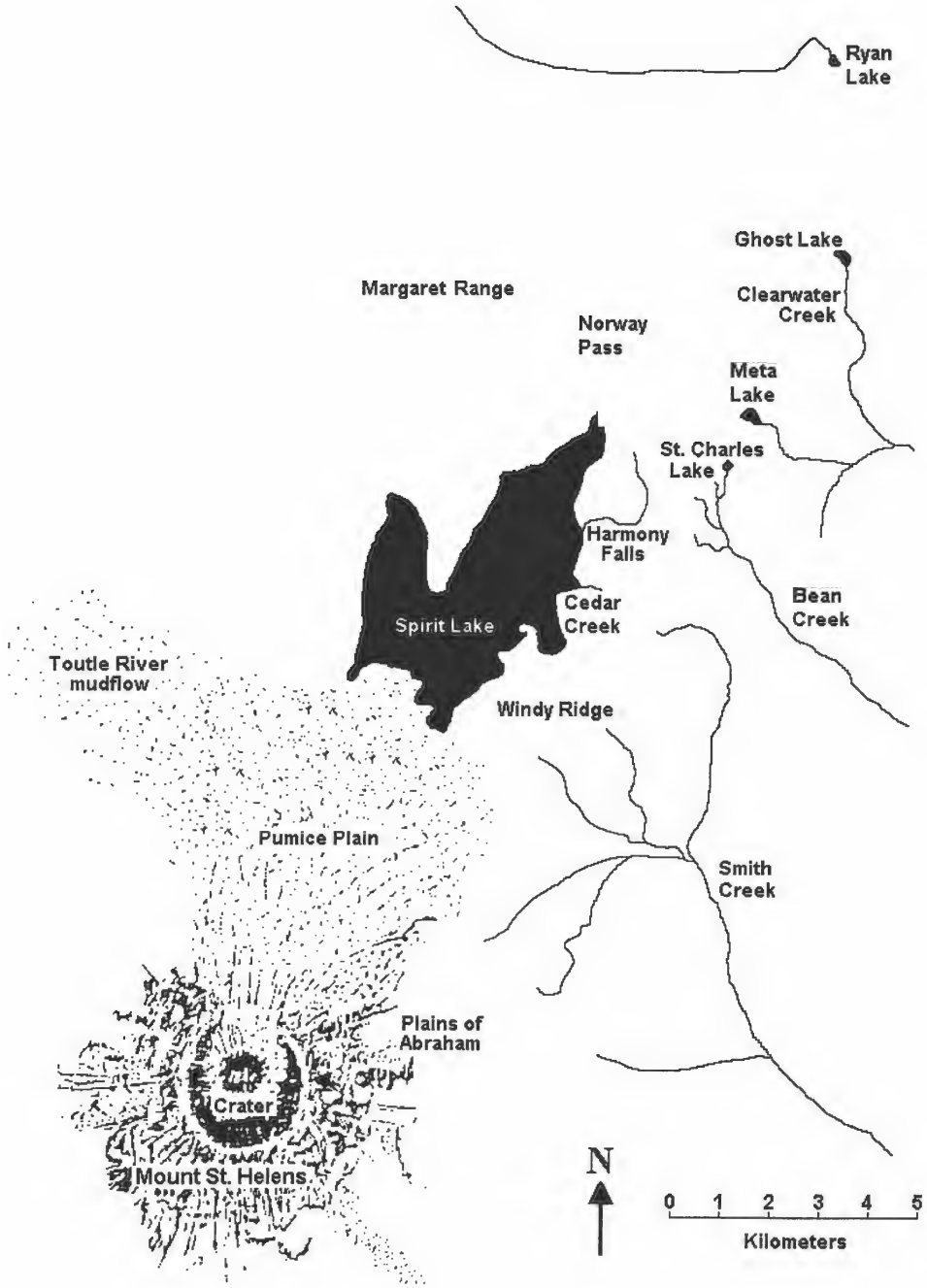

Figure 1. Map of the Mount St. Helens blast zone.

and wetlands occur in low gradient stretches of associated streams (Halpern et al. 1990), but all trees surrounding the lakes were killed during the eruption. In contrast, Ghost Lake (1154 m elevation, 22 km north of the crater) and Clearwater Creek (1349 m elevation, 21 km north of the crater) have both standing dead trees and intact pre-eruption forest on their banks with wetlands that were little altered by the eruption.

Sampling

We sampled wetlands during the summers of 1993 and 1994 by establishing 220 100-m^2 plots. Based on the investigators knowledge of the study area, wetlands were selectively chosen to adequately reflect the range of wetland vegetation, environments, and disturbance intensity described in the previous section. An area was determined to be wetland if the soil was saturated for more than three weeks during the growing season, roughly June to September on Mount St. Helens (del Moral and Bliss 1993). Soil saturation was determined by repeated visits to suspected wetland sites. Wetlands in the blast zone on Mount St. Helens contain large areas of uniform vegetation and zonation is not evident. Circular 100-m^2 plots were selected to sample homogeneous vegetation, except for linear wetlands located along creeks, which were sampled with 5 m x 20 m rectangles. Wetland vascular vegetation data consisted of percent cover of each species. Cover values were estimated by using a 0.25 m^2 PVC frame with strings delineating 25 100 cm^2 squares, thereby allowing for the determination of cover values to the nearest 0.01 m^2 for species with less than 1% cover in a plot. For plants with less than 5% cover, cover values were estimated to the nearest 0.1%. Cover was estimated to the nearest 1% up to 25% cover; and, in 5% increments thereafter. Elevation was determined from contour maps; slope was converted to a 5 state scale (level to steep), and aspect was converted to an exposure scale of 1 = protected, north to 7 = south, exposed, after Whittaker (1960). Nomenclature follows Hitchcock and Cronquist (1976).

Nominal variables were used to characterize the following five wetland types: wetlands with ephemeral water; wetlands with permanent, shallow, standing water; seasonal streams; permanent streams; and pond or lakes. Water depth was not measured because it varies daily and/or seasonally in many of these wetlands. Spring waters were discriminated by touch for two nominal water temperature variables: hot and cold. Substrate was characterized by nominal variables for stable or unstable (unstable sites are subjected to active substrate movement by snow melt in the spring).

Site disturbance intensity was characterized by four disturbance levels as follows: 1 = wetlands surrounded by standing dead trees and with surviving ground vegetation; 2 = wetlands surrounded by fallen dead trees and with some surviving ground vegetation; 3 = wetlands where aboveground vegetation was eliminated, but some belowground plant organs survived; and 4 = newly formed wetlands on primary successional post-eruption substrates. Thus, plots in Disturbance Levels 1 to 3 are secondary successional, whereas those in Disturbance Level 4 are primary successional (i.e., the Pumice Plain). Some plots in Disturbance Level 1 appear to be composed of climax perennial wetland vegetation and are primarily recovering from biomass loss without large changes in species composition.

Data Analysis

Four vegetation analysis techniques were conducted to elucidate vegetation patterns within the blast zone. First, in order to distinguish the wetland plant communities, TWINSPAN cluster analysis was used based on species cover (Hill 1979). For each community, mean species cover, species richness, and diversity (Shannon-Wiener index, base e) was calculated.

Detrended Correspondence Analysis (DCA) was used to obtain indirect ordinations (Hill and Gauch 1980). An indirect ordination yields an ordination diagram that shows the degree of similarity in species composition between plots, or the degree of similarity of species distributions within plots. As species distributions diverge, the distances between points on the species ordination diagram increase. First, three DCAs were conducted: the entire data set, primary successional substrate plots, and secondary successional substrate plots were analyzed. Species cover percentages were log-transformed to improve plot spread in ordination space, and infrequent species were downweighted. Downweighting decreases the influence of a species on the outcome of the ordination. Finally, a fourth DCA was conducted in order to assess the relationship between the four disturbance levels. To do this, each plot was represented by its disturbance level in the DCA.

Spearman rank correlation tests were used to make comparisons between the five wetland types (Zar 1984) and to determine how important the wetland types are in structuring the vegetation in the primary and secondary successional areas. Spearman's test determines the degree of correlation between two wetland types, i.e., if there is a significant result the two wetland types have similar vegetation. To complete this analysis, the cover of each species in the plots that comprise each wetland type were averaged and these average values were ranked and assigned a score based on their ranked position. The outcome was corrected for ties in the ranks, and then tested by Spearman's test.

Relationships between the environmental variables and the plot and species data were explored by Canonical Correspondence Analysis (CCA, ter Braak 1990). CANODRAW and CANOPOST graphics were used, which produce ordination biplot diagrams that show the relationship between plots or species and environmental variables (Smilauer 1993). On the biplots, Axis I represents the direction of the greatest amount of variation and Axis II represents the second greatest amount of variation in the data set. CCA determines the percentage of variability in species composition of the plots that can be explained by the environmental variables.

The entire data set was analyzed by CCA to determine overall patterns, and subsequent analyses were conducted on plots in both primary and secondary successional environments. In order to assess the contribution of each environmental variable in determining vegetation structure, interset correlations and t-values for each variable are examined. Interset correlations are the correlation of each environmental variable with the CCA axes. The t-values of each environmental variable are compared with the Student t-distribution; a variable may contribute significantly to vegetation structure if it greatly exceeds the appropriate critical value (i.e., $t>3$). Thus, environmental variables that contribute significantly to observed patterns were inferred (Jongman et al. 1987, ter Braak 1990). Note that variables that have high correlations with the CCA axes do not necessarily contribute significantly to observed patterns. In addition, in CCA the relationship between the species data and the environmental data can be tested to determine if the relationship is stronger than relationships generated randomly by using the Monte Carlo test (ter Braak 1990). This was tested for the first axes and all the axes combined (called the trace). In all of the CCAs, species cover percentages were log-transformed and infrequent species downweighted. This was done to improve species spread on the ordination diagrams. Finally, a CCA was conducted using wetland type as the only environmental variable. This allowed us to determine the importance of the relationship between wetland types and the wetland plant communities.

Geographic position has been found to play a role in determining which species colonize a site (Primack and Miao 1992; del Moral and Bliss 1993). Borcard et al. (1992) outlined how CCA can separate environmental variation from variation in the species data caused by spatial factors. Spatial positions of the plots were assigned by mapping the location of each plot on a grid of squares with 25 east to west rows, (X), and 16 north to south columns, (Y). Thereby, each plot had a X and Y location and each square represented 0.64 km^2. In order to assess the importance of complex spatial patterns, the matrix of two dimensional coordinates, X and Y, was expanded into a cubic trend surface regression by adding locations represented by X^2, XY, Y^2, X^3, X^2Y, XY^2 and Y^3. These nine spatial variables were analyzed using "forward selection of explanatory variables", a multivariate extension of stepwise regression. Species data were analyzed by the following traits: (a) constrained by the environment after spatial factors are removed, i.e., nonspatial environmental variation, which is the portion of the species variation that can be explained by the environmental variables independent of any spatial structure, (b) constrained by spatial factors after removing environmental effects, i.e., spatial patterns in the species data that are not shared by the environmental data, (c) constrained by spatially structured environmental variables, i.e., spatial structuring in the species data that is shared by the environmental data, and (d) unexplained variation, which includes variation due to unmeasured environmental variables and stochastic factors (Borcard et al. 1992).

Results

Plant Communities

Twenty-four wetland plant communities were distinguished by TWINSPAN analysis (Tables 1 and 2; species composition of each plant community available from the first author upon request).

TABLE 1. Number of plots, successional status (1 = primary, 2 = secondary), mean total percent cover of all species, species richness and diversity (Shannon-Wiener index, base e) of 24 wetland communities from the blast zone of Mount St Helens.

Plant Communities	Sample Size	Succ. Status	% Cover	Species Richness	Species Diversity
1. Aquatic vegetation	11	1,2	69	6.8	0.60
2. *Equisetum fluviatile* wetland	6	2	88	15.8	0.68
3. *Carex interrupta* wet meadow	18	2	111	19.9	1.51
4. *Carex aquatilis-Carex lenticularis* wet meadow	19	2	99	13.7	1.31
5. *Carex canescens* wet meadow	6	2	97	18.2	1.89
6. Disturbed herbaceous streambanks	17	1,2	27	19.9	1.91
6a. Primary successional dist. herb. streambanks	2	1	28	14.5	1.36
6b. Secondary successional dist. herb. streambanks	15	2	27	20.6	1.98
7. *Rubus spectabilis* thickets	1	2	120	26.0	2.22
8. *Alnus sinuata* thickets	5	2	37	22.5	2.02
9. Secondary succ. *Salix sitchensis/Equisetum arvense*	21	2	46	25.3	1.76
10. Primary succ. *Salix sitchensis/Equisetum arvense* A	4	1	63	13.8	0.78
11. Primary succ. *Salix sitchensis/Equisetum arvense* B	11	1	42	15.7	1.18
12. *Salix sitchensis* primary successional wetlands	23	1	39	14.3	1.16
13. *Salix sitchensis/Carex mertensii* wetlands	5	1	51	19.6	1.27
14. Primary successional *Equisetum arvense* wetlands	18	1	47	11.2	0.83
15. *Juncus bufonius* wetlands	7	1	48	10.0	0.94
16. *Juncus articulatus* wetlands	4	1	75	10.3	1.01
17. *Juncus drummondii* wetlands	3	1	14	7.3	1.04
18. *Juncus tenuis* wetlands	1	1	62	9.0	0.63
19. *Juncus ensifolius* wetlands	6	1	69	13.0	1.33
20. *Typha latifolia* wetlands	12	1,2	91	10.5	1.14
20a. *T. latifolia* primary successional wetlands	10	1	87	10.8	1.21
20b. *T. latifolia* secondary successional wetlands	2	2	111	9.0	0.82
21. *Scirpus americanus* wetlands	1	1	46	10.0	1.14
22. *Epilobium watsonii* wetlands	9	1	65	12.0	1.15
23. *Epilobium angustifolium* wetlands	4	1	10	13.0	1.56
24. *Calamagrostis canadensis* wetlands	9	1	6	16.8	1.96

In a few cases, communities occurred in both primary and secondary successional substrates, however, in most cases species composition differed significantly between primary and secondary successional areas. Most widespread species, with the exception of *Salix sitchensis* and *Equisetum arvense*, were confined to either primary or secondary successional substrates. For example, *Juncus* meadows only occurred in primary successional areas, while *Carex* meadows were only in secondary successional areas.

In the DCA analyses, aquatic vegetation plots (composed of submerged or floating-leaved vegetation) were removed from the analyses due to high dissimilarity with the other communities. The DCA of the entire data set comprised 203 plots and 204 species. The first two axes of the DCA ordination explain 9.3 and 8.3% of the variance in the species data, respectively. Thus, the axes explain only a small percentage of the variation in the species data. Axis I in this ordination is 4.7 half-changes long, which is indicative of a data set with a wide range of species composition. In the primary successional data set (116 plots [one outlier plot removed] and 104 species), the first two axes account for 14.4 and 9.9% of the variance, respectively (Figure 2). In the secondary successional data set (86 plots and 177 species), these axes account for 11.7 and 9.0% of the variance, respectively (Figure 3).

Disturbance levels separated moderately well in ordination space (Figure 4). Primary succession plots (Disturbance Level 4) and heavily impacted plots (Level 3) were separated from Levels 1 and 2 along Axis I. Levels 1 and 3 are distinct from Levels 2 and 4 along Axis II.

TABLE 2. Descriptions of 24 wetland communities from the blast zone of Mount St Helens.

Plant Community[1]	Occurrence	Common Species[2]	Notes
1. Aquatic vegetation	Occurs in deep water in all the ponds and lakes examined.	*Potomogeton foliosus* *Potomogeton natans* *Ranunculus aquatilis*	Floating leaved and submerged vegetation. The alga *Chara* is common.
2. *Equisetum fluviatile* wetland	Only occurs in deep water at Ryan Lake.	*Carex aquatilis* *Carex brunnescens* *Typha latifolia*	*Equisetum fluviatile* occurs in deep water. Most of the other species occur on the pond shore.
3. *Carex interrupta* wet meadow	Occurs in low disturbance wetland areas by Ghost Lake and along Clearwater Creek.	*Calamagrostis canadensis* *Equisetum arvense* *Juncus ensifolius* *Salix sitchensis* *Viola glabella*	*Salix sitchensis* is often co-dominant. *Eriophorum angustifolium* occurs occasionally.
4. *Carex aquatilis-Carex lenticularis* wet meadow	Most common along the shore of Meta Lake.	*Equisetum arvense* *Juncus effusus* *Ranunculus sceleratus* *Salix sitchensis* *Salix sitchensis* and	*Equisetum arvense* is common.
5. *Carex canescens* wet meadow	Occurs along the shore of St. Charles Lake.	*Alnus sinuata* *Equisetum arvense* *Potomogeton foliosus* *Salix sitchensis* *Sparganium emersum* *Typha latifolia*	*Salix sitchensis* is often co-dominant.
6. Disturbed herbaceous streambanks	Occurs in higher elevation heavily disturbed secondary successional sites, such as along creeks in Pumice Plain refugia and the Margaret Range; also in primary successional sites along creeks on the Pumice Plain.	*Carex spectabilis* *Lupinus latifolius* *Juncus mertensianus* *Mimulus lewesii* *Valeriana sitchensis*	These areas are often species rich with more than 20 species per plot. Recovering habitats of this type are much more diverse than recently initiated habitats. Slopes are steep, especially in secondary successional sites.
7. *Rubus spectabilis* thickets	Occurs only on the banks of Ryan Lake.	*Athyrium filix-femina* *Epilobium angustifolium* *Glyceria elata* *Petasites frigidus*	Diverse secondary successional type; cover is high due to dense multiple vegetation layers. This vegetation is common as forest understory in wet sites throughout the Pacific Northwest (Kunze 1994, Christy & Titus 1997).
8. *Alnus sinuata* thickets	Occurs in moist, heavily disturbed secondary successional areas.	*Aruncus sylvester* *Athyrium filix-femina* *Epilobium watsonii* *Salix sitchensis* *Saxifraga arguta*	Understory is diverse with usually more than 20 species in a plot. *Alnus sinuata* thickets are common on primary successional substrates on the Pumice Plain, but only in upland areas.
9. Secondary Successional *Salix sitchensis/Equisetum arvense* wetlands	Found in heavily impacted sites along creeks in Harmony Basin and the Margaret Range, and along the Green River and Bean Creek; also found in less disturbed sites by Ghost and Meta Lakes and Coldwater Creek.	*Alnus sinuata* *Anaphalis margaritacea* *Carex mertensii* *Epilobium watsonii* *Juncus mertensianus* *Mimulus lewesii*	These areas are often species rich with more than 30 species in a plot.

TABLE 2, Continued.

Plant Community[1]	Occurrence	Common Species[2]	Notes
10. Primary Successional *Salix sitchensis/Equisetum arvense* wetlands (Type A)	Occurs across the Pumice Plain in several habitats, usually on moist substrates.	*Agrostis exarata* *Carex limnophila* *Carex mertensii* *Epilobium watsonii* *Juncus mertensianus*	Other species at low cover; understory differs from the secondary successional *Salix sitchensis/Equisetum arvense* type.
11. Primary Successional *Salix sitchensis / Equisetum arvense* wetlands (Type B)	Common in the northern part of the Pumice Plain; occurs most commonly along permanent streams.	*Anaphalis margaritacea* *Epilobium watsonii* *Hypochaeris radicata*	Contains upland invasive species.
12. *Salix sitchensis* dominated primary successional wetlands	Common across the Pumice Plain, usually on the banks of permanent streams; also occurs in the crater.	*Anaphalis margaritacea* *Epilobium angustifolium* *Epilobium watsonii* *Hypochaeris radicata* *Petasites frigidus*	*Equisetum arvense* is not present or only present in trace amounts.
13. *Salix sitchensis/Carex mertensii* wetlands	Occurs in the northern part of the Pumice Plain on ephemeral moist substrates.	*Agrostis exarata* *Alnus sinuata* *Anaphalis margaritacea* *Aruncus sylvester* *Lupinus latifolius* *Luzula parviflora* *Penstemon cardwellii* *Saxifraga ferruginea*	Understory differs from other *Salix sitchensis* types with a greater cover of upland invasive species.
14. *Equisetum arvense* wetlands	Occurs only in the northern part of the Pumice Plain and is the most common wetland type on the Plain.	*Agrostis exarata* *Epilobium watsonii* *Hypochaeris radicata* *Salix sitchensis*	Large areas of wet silt sediments are dominated by monocultures of *Equisetum arvense*; with infrequent occurrences of other species. This vegetation type occurs most frequently in moist and standing water habitats.
15. *Juncus bufonius* wetlands	Low diversity *Juncus bufonius* wetlands cover extensive ephemeral moist areas in the northern part of the Pumice Plain.	*Agrostis exarata* *Equisetum arvense* *Epilobium watsonii*	Often located on moist silt deposits.
16. *Juncus articulatus* wetlands	Habitat is similar to *Juncus bufonius* wetlands.	*Epilobium watsonii* *Equisetum arvense* *Juncus bufonius*	*Juncus bufonius* and *Equisetum arvense* are often co-dominants.
17. *Juncus drummondii* wetlands	Habitat is similar to *Juncus bufonius* wetlands.	*Juncus bufonius*	*Juncus bufonius* is co-dominant.
18. *Juncus tenuis* wetlands	Habitat is similar to *Juncus bufonius* wetlands.	*Equisetum arvense* *Juncus bufonius* *Salix sitchensis*	*Equisetum arvense* is often co-dominant and *Juncus bufonius* is usually common.
19. *Juncus ensifolius* wetlands	Occurs on the north end of the Pumice Plain in ephemeral moist habitats and in standing water and along streams.	*Carex mertensii* *Epilobium watsonii* *Equisetum arvense* *Salix sitchensis*	Not strongly associated with the other *Juncus* species.
20. *Typha latifolia* wetlands	Occurs in standing water on primary successional substrates in the Pumice Plain, and in secondary successional areas along the shores of several of the ponds.	*Epilobium watsonii* *Equisetum arvense* *Juncus bufonius* *Juncus ensifolius* *Salix sitchensis*	This type occurs across the disturbance spectrum. Secondary successional sites are similar to primary successional sites in richness, but are less diverse.

TABLE 2, Continued.

Plant Community[1]	Occurrence	Common Species[2]	Notes
21. *Scirpus americanus* wetlands	Occurs infrequently in standing water across the Pumice Plains.	*Eleocharis palustris* *Epilobium wasting* *Equisetum arvense* *Juncus bufonius*	Associated with hot water springs.
22. *Epilobium watsonii* wetlands	Occurs along both permanent and ephemeral streams on the Pumice Plain.	*Equisetum arvense* *Juncus bufonius* *Salix sitchensis*	The preponderance of *Epilobium watsonii* and the streambank habitat separate this from *Equisetum arvense* and *Juncus bufonius* wetlands.
23. *Epilobium angustifolium* wetlands	Occurs along both permanent and ephemeral streams on the Pumice Plain.	*Anaphalis margaritacea* *Carex mertensii* *Epilobium watsonii* *Mimulus lewesii* *Salix sitchensis*	Occurs in drier habitats and contains more upland invasive species than *Epilobium watsonii* wetlands.
24. *Calamagrostis canadensis* wetlands	Occurs along permanent streams on the Pumice Plain.	*Anaphalis margaritacea* *Epilobium angustifolium* *Epilobium watsonii* *Salix sitchensis*	Diverse primary successional community; this type is composed of both upland and wetland species.

[1] Vegetation types not discussed are as follows: moss-dominated wetlands occur patchily across the Pumice Plains; *Merchantsia* patches occur in seepage areas; *Hypochaeris radicata* dominated wetlands occur on the Pumice Plain and in the crater; patches of *Petasites frigidus* occur in some of the secondary successional areas; algal mats are common along both hot and cold spring runs and in the lakes.

[2] Species composition of each plant community available from the first author upon request.

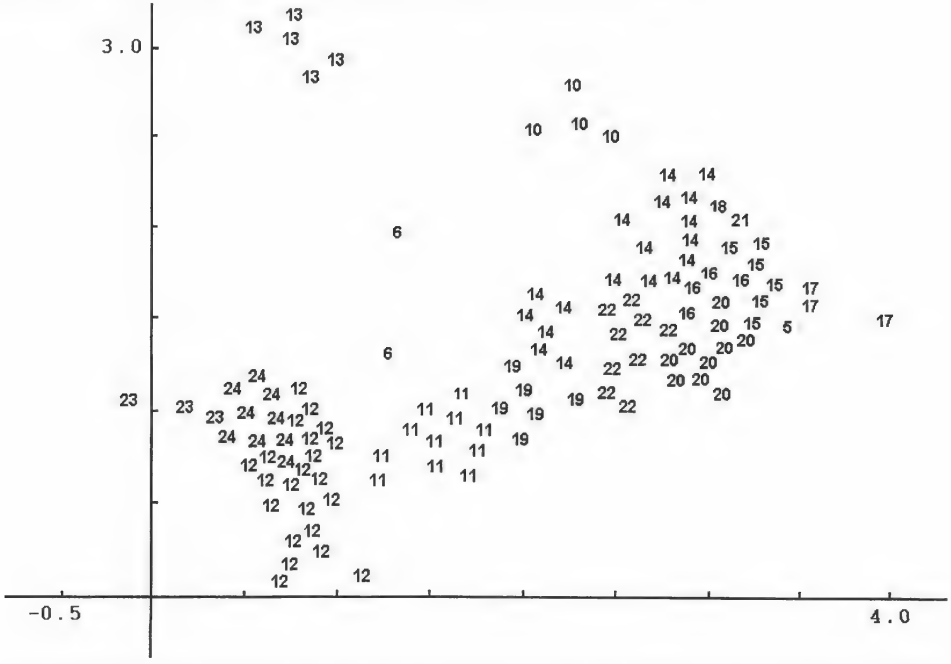

Figure 2. Detrended Correspondence Analysis of primary successional plots. Numbers correspond to communities in Tables 1 and 2.

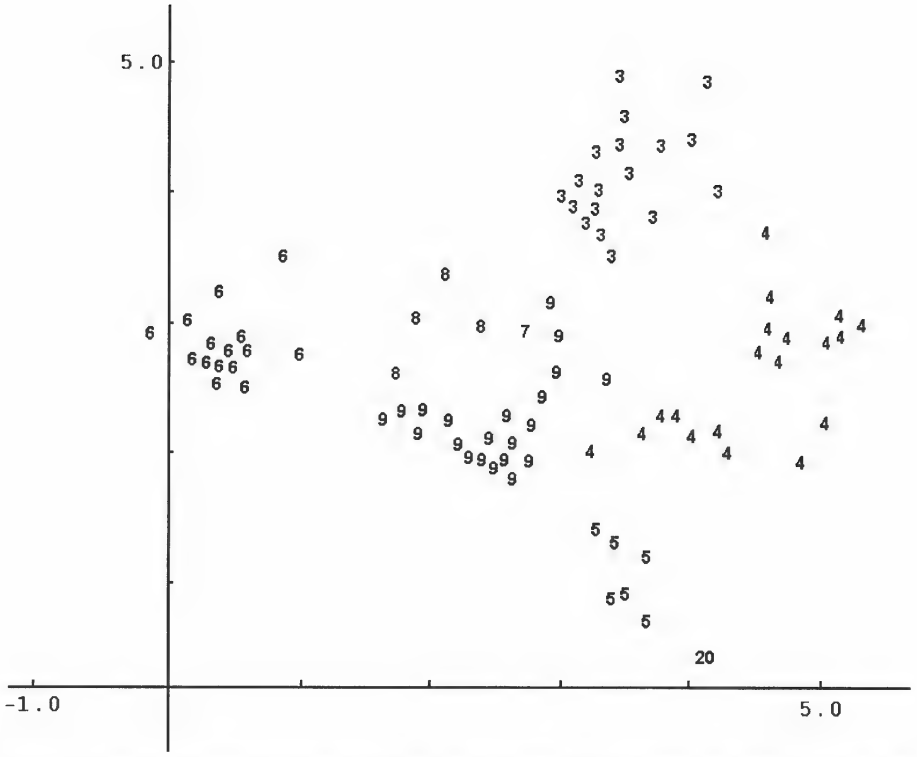

Figure 3. Detrended Correspondence Analysis of secondary successional plots. Numbers correspond to communities in Tables 1 and 2.

Correlations between Vegetation of the Wetland Types

Spearman rank correlations among primary successional wetland types show modest, but significant correlations (Table 3). Vegetation in wetlands with permanent shallow standing water is not significantly correlated to vegetation along ephemeral streams, which contains many upland species. In secondary successional environments wetland types are not correlated, with the exception of ephemeral streams, which are primarily found in heavily impacted sites. If the heavily impacted secondary successional sites (Disturbance Level 3) are removed from the analysis, the relationships do not change; however, the ephemeral stream group then has an insufficient sample size.

Canonical Correspondence Analysis

Entire Data Set. Aquatic plots were distinctive and were removed from the analysis. Of the variability in species composition of the plots, 24.7% can be explained by the environmental variables. For the entire data set, both axis I and the trace are significant as analyzed by the Monte Carlo test (P=0.01); that is, the relationship between the species and environmental data is stronger than randomly generated relationships.

Wetland communities did not segregate in the CCA biplot, indicating that they are not characterized by a consistent combination of environmental variables. The most important environmental variable on axis I, based on interset correlations (Table 4) and t-values, was disturbance level (t = 19.76). Axis II has its strongest relationships with elevation (t = 10.53) and the nominal variable "ephemeral stream" (t = 10.08). Also on axis II, the nominal variable "wet stream", although not highly correlated with axis II, was significant (t = 8.78).

Primary Successional Plots. The CCA of plots on primary successional substrates is shown in Figure 5. Of the variability in species composi-

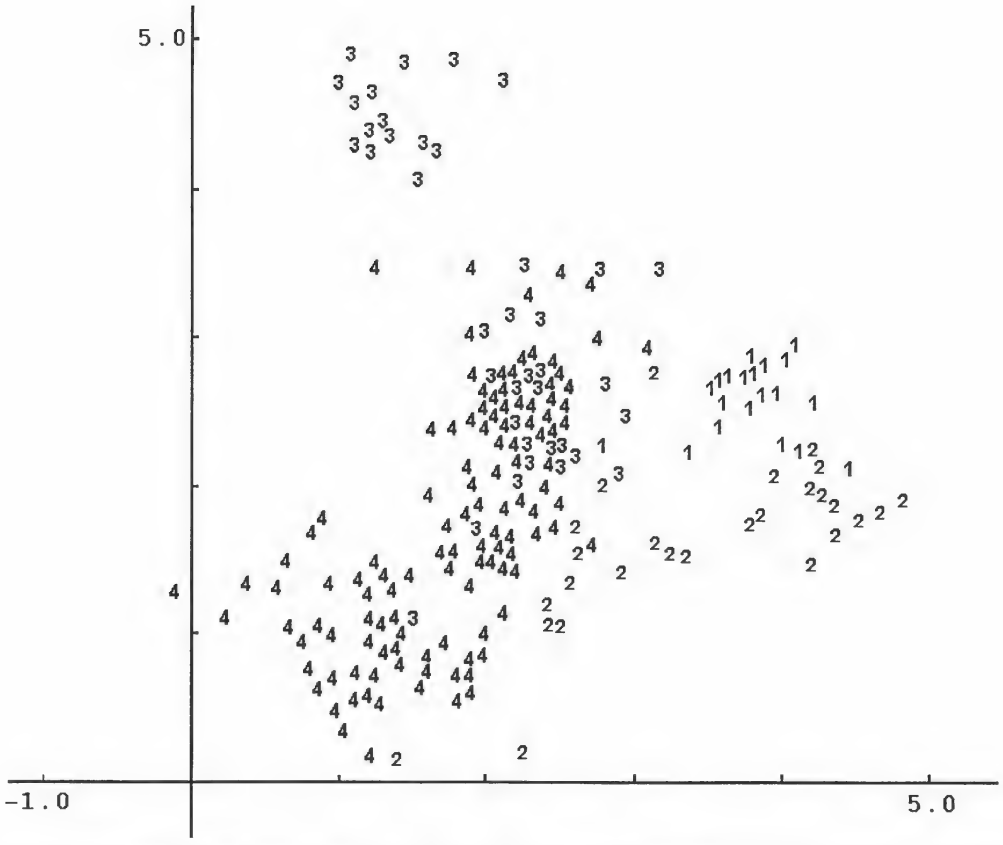

Figure 4. Detrended Correspondence Analysis of all plots. Numbers are the Disturbance Levels. 1=low impact; 2=moderate impact; 3= heavily impacted secondary succession; 4=primary succession.

TABLE 3. Spearman rank correlations between wetland types. The cover of each species in the plots comprising a wetland type were averaged, ranked, corrected for ties in the ranks, and then tested by Spearman's test. A significant result (in bold) indicates that the two wetland types have vegetation that is significantly correlated. In primary successional wetland types, pond was not tested due to small sample size, and in secondary successional wetland types, standing water was not tested due to small sample size.

Wetland Type	Primary Successional	Secondary Successional
moist vs. standing water	**r=0.366 p<0.005**	—
moist vs. ephemeral stream	**r=0.316 p<0.02**	**r=-0.419 p<0.001**
moist vs. permanent stream	**r=0.597 p<0.001**	r=0.170 p>0.1
moist vs. pond	—	r=0.046 p>0.5
standing water vs. ephemeral stream	r=0.174 p>0.1	—
standing water vs. permanent stream	**r=0.555 p<0.001**	—
ephemeral stream vs. permanent stream	**r=0.550 p<0.001**	r=-0.038 p>0.5
ephemeral stream vs. pond	—	**r=-0.258 p<0.01**
permanent stream vs. pond	—	r=0.167 p>0.05

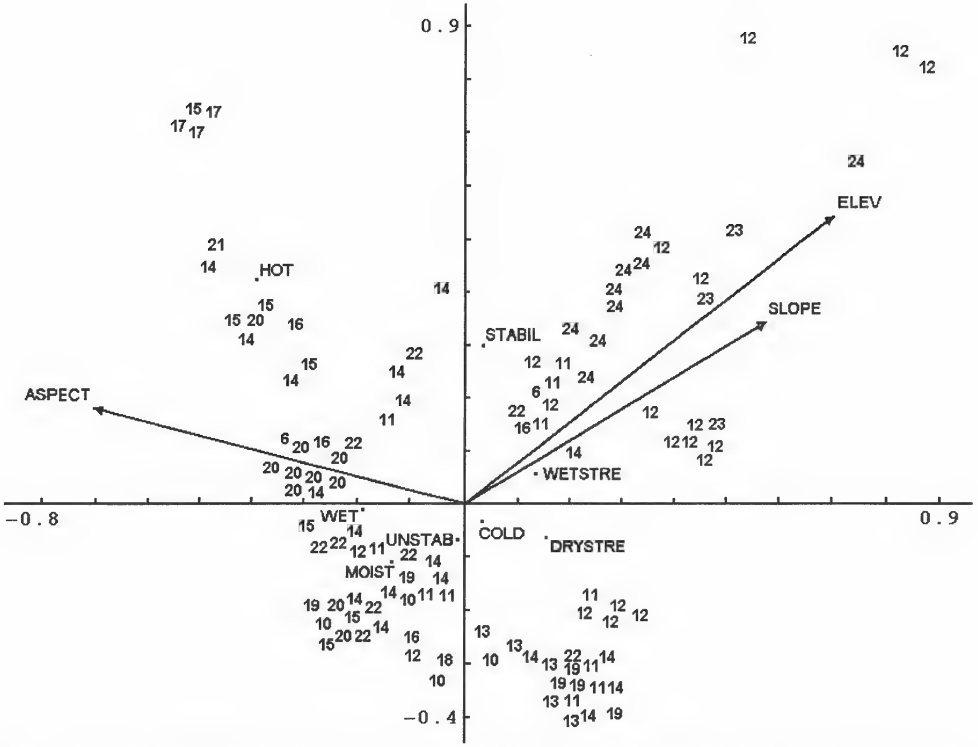

Figure 5. Canonical Correspondence Analysis plot-environment biplot of primary successional plots. Numbers correspond to communities in Tables 1 and 2. Abbreviations of environmental variables are defined in Table 4. See text for interpreting the diagram.

tion of the plots, 19.0% can be explained by the environmental variables. Note that disturbance level is not included in this analysis since all plots are primary successional. Both axis I and the trace are significant (P=0.01, Monte Carlo test). In the ordination biplot diagram, nominal environmental variables are represented by points and continuous environmental variables are represented by vectors. The direction of a vector represents the direction of maximum change of the environmental variable across the diagram and the length of a vector is proportional to the magnitude of change in that direction. The environmental variables that have long arrows are more closely correlated to the vegetation than those with short arrows and are usually more important in influencing community variation. The vector should also be considered as extending back through the origin. A point that represents a plot can be related to each vector by drawing a perpendicular from the line of the vector up to the point representing the plot. Plots with their perpendicular projections near to or beyond the tip of the vector will be strongly correlated with and influenced by that environmental variable, those near the center will be less affected. Also, the position of a vector with respect to an axis indicates how closely correlated the axis is with that environmental factor (Kent and Coker 1992).

Based on t-values for Axis I, the variables elevation, permanent stream and hot water contribute the most to vegetation structure. Elevation, slope and aspect have the highest correlations with axis I (Table 4). Although slope and aspect contribute significantly to the pattern, they are less important than some of the wetland types and water temperature. Axis II is not strongly correlated with any environmental variable, nonetheless elevation and substrate stability contribute the most to this axis. Slopes increase and exposure decreases (i.e.,

TABLE 4. CCA interset correlations of environmental variables with the canonical axes. All analyses were conducted with aquatic vegetation removed. Scores are times 1000. Variables that contribute strongly to the ordination (t>3.0) are in bold. Variables that have high correlations with CCA axes do not necessarily contribute significantly to observed patterns. Thus, large interset correlation values are not necessarily significant.

	All Plots		Primary Successional		Secondary Successional	
Variable	Ax 1	Ax 2	Ax 1	Ax 2	Ax 1	Ax 2
Elevation-ELEV	**106**	**647**	**612**	**369**	**786**	**84**
Slope-SLOPE	110	**403**	507	250	359	86
Aspect-ASPECT	**-334**	-227	**-601**	138	-463	-112
Moist Site-MOIST	-109	**-122**	**-209**	-134	-218	**494**
Wet Site-WET	**281**	-320	**-389**	-6	-107	97
Ephemeral Stream-DRYSTRE	**184**	**455**	144	-50	**771**	**74**
Permanent Stream-WETSTRE	**164**	**256**	436	135	**106**	**152**
Pond-POND	**-494**	**-246**	—	—	**-399**	**-578**
Hot Water-HOT	222	**-266**	**-378**	**338**	—	—
Cold Water-COLD	-222	266	378	-338	—	—
Stable Substrate-STABIL	-294	298	77	393	609	25
Unstable Substrate-UNSTAB	294	-298	-77	**-393**	-609	-25
Disturbance Intensity-DIST	**865**	**-120**	—	—	**-720**	**-503**

more northern aspects) with increasing elevation. Wet and moist sites generally occur at lower elevations, whereas streams occur at higher elevations.

Most of the communities do not segregate in the CCA biplot, indicating one or more of the following: plots comprising each plant community do not belong to a similar set of environmental variables; vegetation is responding to unmeasured variables; and/or, vegetation patterns are stochastic, i.e., the patterns in the vegetation are due to random factors rather than environmental variables. Weak species-environment patterns were further reflected by the common species, in that most of the common species were located near the center of the biplot (not shown), which indicates that they inhabit a variety of environments. Weak tendencies, such as the affinity of *Equisetum arvense* for moist areas and *Salix sitchensis* for seasonal streams, were apparent. Most *Juncus* species cluster around the wet substrate variable.

Secondary Successional Plots. The CCA of plots on secondary successional substrates, including non-aquatic pond vegetation (i.e., emergent vegetation near a pond shore), is shown in Figure 6. Of the plot variability in species composition, 34.7% can be explained by environmental variables. Both Axis I and trace are significant (P=0.01, Monte Carlo test).

Axis I is correlated with elevation (t = 13.19), ephemeral streams (t = 11.50), disturbance (t=7.79), and permanent streams (t = 9.15); substrate stability is not significant (Table 4). Axis II is correlated with ponds, disturbance and moist areas. It is clear from Figure 6 that, with increasing elevation, slope increases, whereas exposure and substrate stability decreases; ephemeral streams are the most common wetland type at higher elevations. Thus, the "disturbed stream" vegetation type is found in a portion of the diagram that illustrates higher elevation, unstable substrate, steep slopes, and ephemeral character.

Plots are strongly clustered in several parts of the CCA biplot (Figure 6). Many communities retain their coherence in the CCA biplot, indicating that the plots comprising each community belong to a similar set of measured environmental variables. *Carex* meadows occupy the left part of the biplot and vary along axis II. *Carex* meadows are usually associated with ponds, except *Carex interrupta* meadows, which often occur in wet areas not associated with ponds. There is a clear distinction between heavily impacted streamside sites and *Carex* meadows, because *Carex* meadows occur in environments that suffered relatively little disturbance from the eruption. Unlike the primary successional CCA, *Salix sitchensis* and *Equisetum arvense* do not occur in such a

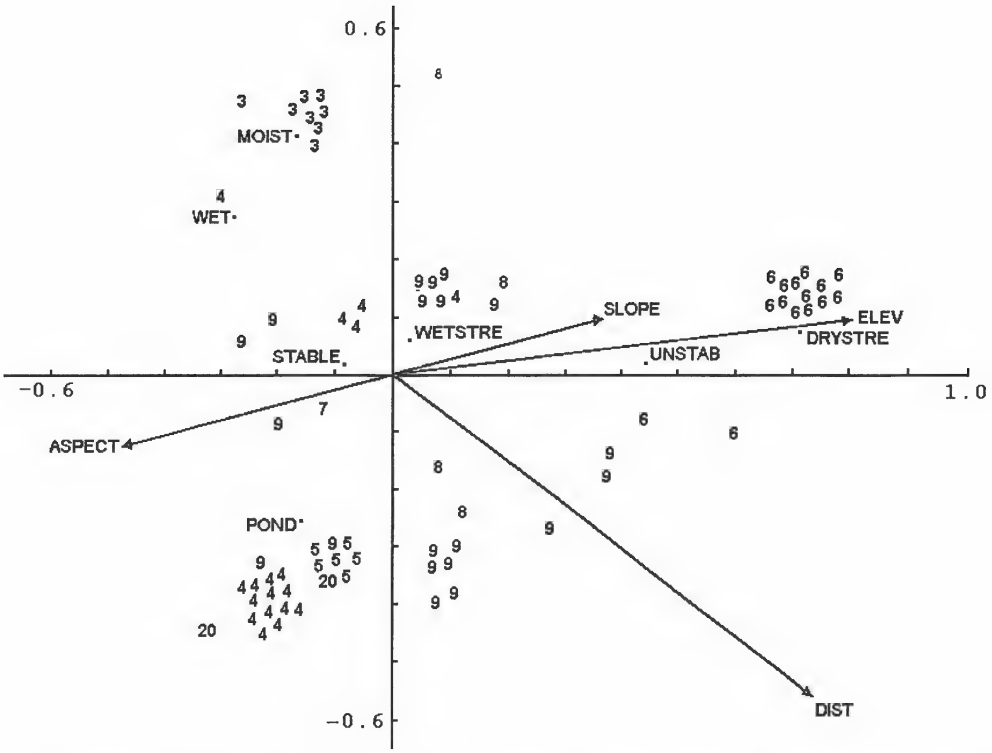

Figure 6. Canonical Correspondence Analysis plot-environment biplot of secondary successional plots. Numbers correspond to communities in Tables 1 and 2. Abbreviations of environmental variables are defined in Table 3. See text for interpreting the diagram.

wide array of environments and are not in the center of the biplot.

Wetland Types in CCA. CCAs were conducted on primary and secondary successional data using only wetland type as the environmental variable. Results were tested by the Monte Carlo test. In both primary and secondary successional communities, wetland type was significant (primary successional first axis P=0.01, trace P=0.01; secondary successional first axis P=0.01, trace P=0.01). This indicates that the relationship between wetland type and species distribution is different from a random distribution, and that there is a significant relationship between wetland type and vegetation patterns.

Spatial Analysis. For the three data sets (complete, primary successional and secondary successional), forward selection indicated that most spatial variables were significant. Although the amount of variability explained by spatial variables was not large, it was comparable to the variability explained by measured environmental factors alone (Table 5). However, multicollinearity between the spatial variables was high. "Inflation values" >20 in the CCA output indicate high multicollinearity between environmental variables. If only those spatial variables which have low multicollinearity are used, explained spatial variability is reduced by about one-half. If inflation values are reduced below 20, the following spatial variables are retained: Y, X^3 and XY^2 for the complete data set; X^3, X^2Y and Y^3 for the primary succession data set; and Y, X^3 and XY^2 for the secondary successional data set. If only X and Y are used, explained spatial variability is considerably reduced.

In these analyses environmental, spatial, and spatially-structured environmental sources of

TABLE 5. Variance partitioning of wetland vegetation from Mount St. Helens. The variation due to environmental factors after removing the effect of the geographical matrix, the variation due to the geographical matrix after removing the effect of the environmental variables, spatially structured environmental variation, and the remaining unexplained variation are partitioned. Spatial variables used were determined by forward selection. Spatial variables were: all plots (X ,Y, X^2, XY, Y^2, X^3, X^2Y, XY^2), primary successional (X ,Y, X^2, Y^2, X^3, X^2Y, Y^3), secondary successional (X ,Y, X^2, XY, Y^2, X^3, X^2Y, XY^2, Y^3).

	% Variance partitioned		
Source of Variation	All Plots	Primary Successional	Secondary Successional
environmental	11.7	11.2	18.5
spatial	13.4	17.1	16.6
spatially structured environmental	11.0	10.5	16.3
unexplained/stochastic	64.0	61.2	48.7

variation account for 35-50% of vegetation structure. Measured environmental factors are more important in the secondary successional vegetation than in the other analyses. Unexplained variation is high in all three analyses, although it is less than 50% in the secondary successional analysis. Unexplained variation includes variation due to unmeasured environmental factors and stochastic factors, such as seed dispersal.

Discussion

Communities

Wetland communities in the less impacted areas of this study also occur at similar elevations throughout the region where there is suitable substrate (Franklin and Dyrness 1988, Kunze 1994, Titus et al. 1996, Christy and Titus 1997). Likewise, vegetation similar to the primary successional wetland communities on the Pumice Plain is found in highly disturbed wet areas from sea level up to the elevation of the Pumice Plain throughout the region (Titus et al. 1996, J. Titus, pers. obs.). For example, wetlands dominated by *Epilobium watsonii* and *Salix sitchensis* occur in wet, logged sites, *Juncus bufonius* and *J. tenuis* are found along logging roads, and *Equisetum arvense* occurs in wet areas around road construction.

The most species rich and diverse communities found in this study are the secondary successional *Alnus, Salix/Equisetum,* and *Rubus spectabilis* thickets. This is due to the rich assemblage of understory herbaceous species. These communities are located in disturbance prone sites, such as streambanks, and both early and late successional species occur in the understory. Primary successional *Salix* communities are less diverse because they contain fewer understory species, i.e., the later successional species are not present. The *Salix sitchensis/Carex mertensii* community is more diverse than the other primary successional *Salix* communities because of the occurrence of both upland and wetland pioneer species in the understory; this is due to the fact that *Salix sitchensis/Carex mertensii* occurs in drier substrates than the other *Salix* communities.

Many pioneer species most commonly found in uplands colonized both wet and dry areas across the Pumice Plain. These species have wide ecological amplitudes and can inhabit many different kinds of sites if the site is unoccupied (Grime et al. 1988, del Moral et al. 1995, Titus et al. 1998). These species are represented in high densities in the seed rain (del Moral and Bliss 1993, del Moral and Wood 1993a). For example, wet areas in high impact sites often contain species such as *Anaphalis margaritacea*, *Epilobium angustifolium* and *Hypochaeris radicata*, however, it is unlikely that these will persist in Pumice Plain wetlands. These species are less common in wetlands in the low impact areas. The preponderance of *Equisetum arvense* dominated wetlands on the Pumice Plain may be due to the aggressive clonal spread of this species combined with substrate instability, which make *E. arvense* sites difficult for other species to colonize. No information regarding the density of *E. arvense* spores in the seed rain is available, probably because the spores are too small to be documented in most seed traps.

A major difference between primary and secondary successional areas is the predominance of *Juncus* dominated wetlands on the Pumice Plain and the predominance of *Carex* dominated wetlands in less disturbed areas (Table 1 and 2). *Carex* species form wet meadows in relatively undisturbed areas throughout the Cascade Range. *Juncus* species, with the exception of *J. ensifolius*, generally vegetate wetlands in disturbed sites throughout the region. It is possible that the *Carex* species have not invaded Pumice Plain wetlands due to

dispersal limitations, but upland *Carex* species, *e.g.*, *Carex mertensii* and *Carex limnophila*, are widespread across the Pumice Plain (Titus et al. 1998). Thus, it is more likely that the characteristics of Pumice Plain wetlands, such as high substrate instability, are not amenable to wetland *Carex* species.

Disturbance Level

The intensity of disturbance from the eruption strongly influenced species composition within our study area. During the eruption, vegetation was completely destroyed in primary successional sites and heavily impacted in Disturbance Level 3 secondary successional sites. Since the eruption, some primary successional sites have developed vegetation that resembles that of heavily impacted secondary successional sites and the boundary between these two disturbance levels (levels 3 and 4) overlaps in the DCA ordination (Figure 4). This overlap is caused by primary successional *Salix* thickets that resemble heavily-impacted secondary successional *Salix* thickets. Nevertheless, most primary successional sites differ from heavily impacted secondary successional sites; this is primarily due to later successional and forest species that sprouted from rootstock that survived the eruption (del Moral et al. 1995, Titus et al. 1998) and differences in substrate features. Many Disturbance Level 3 secondary successional sites are ephemeral streams on steep slopes, whereas the Pumice Plain is relatively flat and offers a wider variety of wetland types. Disturbance Level 2 plots are often floristically similar to Disturbance Level 1 plots, particularly those dominated by *Carex* species.

Wetland Types

Wetland types were found to be more important in structuring the vegetation in secondary successional plots than in primary successional plots (Table 3). This may be a result of wide ecological amplitudes of many primary successional species that can occupy any moist site. For example, several species (e.g., *Agrostis exarata, Equisetum arvense*, and *Juncus bufonius*) are prevalent in plots across all wetland types, and their inclusion prevent wetland types and communities from segregating clearly in the DCA ordination (Figure 2). As succession proceeds, it is likely that these widespread species will become restricted to certain environments or disappear. Species such as *Juncus bufonius* may become less common when substrates stabilize and other species invade. Wetland types in secondary successional sites differ from each other in species composition and the plant communities have few species in common. Species in these communities, when compared to those that dominate primary successional wetlands, appear to have relatively narrow distributions, i.e., these species occur in fewer communities.

Succession

Not all of the sites in this study are necessarily successional, rather some may be merely recovering from biomass removal. For example, *Carex* meadows are stable communities. These sedges apparently survived the eruption under ice and sprouted through accumulated ash. In contrast, highly disturbed sites with *Salix sitchensis* and *Alnus sinuata* thickets will probably change in the coming decades as shrub cover increases. Eventually, these communities may resemble the high shrub cover sites observed in low impact areas. Herbaceous wetlands on primary successional sites will change in ways that are difficult to determine at present. It is likely that *Typha latifolia* will dominate some sites and *Salix sitchensis* will eventually dominate others (Keddy 1989, Tu et al. 1998). Clonal species such as *Equisetum arvense* and *Typha latifolia* may retain site dominance indefinitely (Keddy 1989, Tsuyuzaki 1989, Prach and Pysek 1994). Unstable sites may continue to be dominated by *Equisetum arvense* and/or *Juncus bufonius* for many years if substrates do not stabilize. Thus at present, there is little evidence that primary successional wetland sites are undergoing directional succession towards relatively undisturbed wetland communities and little reason to believe that they soon will. Most of the Pumice Plain will eventually become forest that will resemble the pre-eruption Pumice Plain (Kruckeberg 1987). Because of the geologically unstable nature of the Pumice Plain, hydrologic changes may cause some substrates to become drier through time. Wetlands that remain may become *Thuja plicata* dominated forest, which occurs elsewhere in the region (Franklin and Dyrness 1988, Kunze 1994, Titus et al. 1996, Christy and Titus 1997). If the shore of Spirit Lake stabilizes, the vegetation may eventually resemble pond shore vegetation found in low impact sites, although there is no evidence of this at present.

Contribution of Spatial and Environmental Variables

In upland areas on Mount St. Helens, geographic position plays an important role in determining which species colonizes a site (del Moral and Bliss 1993). Spatial analyses enable a partition to be made between environmental, spatial, spatially structured environmental, and undetermined components (Borcard et al. 1992). In the complete and secondary successional analyses, disturbance intensity is highly correlated with both the X and Y factors. This is because disturbance decreases with increasing distance from the volcano in all directions. Likewise in these two analyses, spatial variables are highly correlated, which indicates that similar patterns are explained by both X and Y variables. However, forward selection indicated that, even with high correlations, a large number of spatial variables were significant in structuring vegetation patterns. A reason for this is the patchy distribution of wetland complexes across the landscape. Each of these wetland complexes was sampled by several plots, causing groups of vegetatively similar plots to be highly clumped in spatially scattered wetland locations. This clumping of vegetatively similar plots may cause a large number of spatial variables to exhibit significance. The amount of variation in the vegetation attributed to spatial variation is most likely due to this landscape effect. Thus, although a large number of spatial variables are significant, that does not mean that they are all important in structuring the vegetation. In any case, the amount of variation due to the spatial and environmental variables are similar and both are relatively unimportant in structuring the vegetation (Table 5). Unexplained variation (variation due to unmeasured environmental variables and/or stochastic factors) was found to explain 61.2% of the variation in the primary successional plots, as opposed to 48.7% for secondary successional plots (Table 5).

Environmental variables that are important in mature wetlands, such as soil chemistry, are unlikely to be important in early successional landscapes, where soils are extremely nutrient poor (Tu et al. 1998, Titus unpubl. data). Thus, it is likely that stochastic factors were initially important in the colonization of primary successional wetlands, i.e., a wetland is colonized by a particular species based upon the random chance of a propagule of that particular species landing in the wetland. At present, many of these wetlands are densely vegetated, much more so than most upland sites (del Moral et al. 1995) and therefore other factors, such as competition, are also important. However, in high-disturbance primary successional wetlands, such as unstable streambanks and areas of frequent sediment deposition, stochastic factors, such as seed dispersal, may still be important for establishment because open sites remain plentiful. In these areas chance would favor the locally prevalent species.

Stochastic factors are unlikely to be important in structuring low impact sites, because vegetation has occupied these sites for long periods of time and vegetative cover is high. Thus, it is probable that unmeasured pre-eruption environmental variables, rather than chance, are important in the low impact sites and are responsible for most of the unexplained variation.

In upland primary successional studies, it has been posited that initial species assemblages are *ad hoc* and may be novel. Invading species have broadly overlapping tolerances and therefore many species could potentially occupy a microsite (del Moral and Wood 1993b, del Moral et al. 1995). Establishment has been attributed to stochastic factors operating through a lottery model (Sale 1977, Lavorel and Lebreton 1992). Unlike upland primary successional sites, where species generally cannot exclude other pioneers from their vicinity (del Moral et al. 1995), in wetlands plants can exclude other pioneers. This is due to the rapid achievement of high cover in the wet environment via prolific seed production and clonal growth. Thus, it is unlikely that a carousel mechanism (van der Maarel and Sykes 1993), where different species successively occupy the same microsite, will occur.

In the wetlands studied here, most of the primary successional communities are not novel, but are similar to wetland species assemblages found in heavily disturbed sites throughout the region. If the unexplained variation in communities was largely determined by stochastic factors, would it be possible that similar assemblages would develop in disturbed sites throughout the region? On the Pumice Plain, initial species composition may have been stochastic from the pool of wetland species that have propagules in the seed rain, i.e., founder effects are important. That is, seed and clone production by locally established species would quickly outweigh any long distance

dispersal by species not locally established (Moody and Mack 1988, del Moral and Bliss 1993, Stöcklin and Bäumler 1996). Thus, where a species establishes and subsequently becomes dominant is due to the chance processes of dispersal and not due to environmental variables. Because of the limited pool of wetland species in the seed rain, communities that emerge via the stochastic dispersal process are similar to wetland vegetation throughout the region. The particular location of an *Equisetum arvense, Salix sitchensis* or *Juncus bufonius* wetland is stochastic because these species can colonize a wide variety of sites, and because of the relatively small available species pool similar wetland assemblages occur elsewhere. Thus, these wetland communities are found throughout the region wherever a disturbance occurs. However, future changes in vegetation composition will be driven by factors such as environmentally mediated competition.

Conclusion

We conclude that environmental factors were not of great importance in the species assembly of wetland communities on the Pumice Plain. Stochastic factors are important on the Pumice Plain and are linked with a small species pool of potential dominants, which yield common and recognizable communities with little linkage to environmental factors. Thus, similar sites yield different communities. Vegetation development in the future will be strongly determined by initial founder effects. In low impact areas, unmeasured environmental variables appear to be of greater importance.

Acknowledgments

Thanks to S. Tsuyuzaki, J. Bishop and S. Moore for assistance in the field. J. Leps assisted with data analysis and the facilities of the Faculty of Biology, University of South Bohemia, Ceske Budejovice, Czech Republic were invaluable. J. Leps, P. Smilauer, J. Christy, E. Rykiel Jr., and an anonymous reviewer greatly improved the manuscript. Many species were identified by M. Arnot, A. Yen, S. Gage, S. Moore and J. Christy. A grant from the Washington Native Plant Society made this research possible. NSF Grants BSR-89-06544 and DEB-9406987 to R. del Moral helped support this research.

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Received 4 September 1998
Accepted for publication 18 June 1999

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Fire History in Douglas-fir and Coast Redwood Forests at Point Reyes National Seashore, California

Abstract

Historical variability in fire regimes and forest age structures is necessary reference information for management of vegetation and landscape patterns in naturally managed ecosystems. In this study, we reconstructed fire history and forest age structure at Point Reyes National Seashore on the central California coast to document changes in forest conditions over the past ca. two centuries. Surface fire history was reconstructed from dendrochronologically-crossdated fire-scarred trees in two stands of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and one stand of coast redwood (*Sequoia sempervirens*). Age structure in an approximately 2000 ha area of Douglas-fir forest was examined for tree recruitment patterns. Reconstructed mean surface fire intervals and Weibull median probability intervals ranged from ~ 7 to ~13 years. Fires generally occurred late in the growing season or after growth had ceased for a year. Spatial patterns of historic fires and those reconstructed from the fire-scar record document often widespread fires in the central Olema Valley. Likely many, if not most, of the fires reconstructed from Point Reyes were ignited by humans given the long history of intensive use of this area, first by the Coast Miwok and later by European ranchers. Age structures of stands suggest that much of the Douglas-fir overstory is multiaged with little evidence of stand-replacing fire or other disturbance events. Ages of trees in Douglas-fir stands document increasing landscape coverage of Douglas-fir forest at Point Reyes and hardwood recruitment under older Douglas-fir canopies, and suggest that loss of surface fires is having cascading effects on landscape vegetation patterns, community relationships, and probably related ecosystem processes.

Introduction

Changes in fire regimes over the past century are well documented for many areas, especially in ecosystems that experienced frequent, episodic surface fires prior to widespread non-Native American settlement beginning in the western US in the 1800s (Agee 1993, Swetnam 1993, Covington and Moore 1994, Brown and Swetnam 1994, Swetnam and Baisan 1996, Barrett et al. 1997). Livestock grazing, geographical fragmentation caused by roads and fences, and fire suppression have resulted in the cessation of surface fires in these ecosystems. Cessation of surface fires has, in turn, led to often profound changes in forest and landscape vegetation patterns. Frequent surface fires killed tree seedlings and saplings before they could become established in a forest overstory or on grassland or shrubland margins. Increases in tree density or landscape coverage after fire exclusion have led to concurrent losses of understory biomass and species diversity and shifts in biogeochemical cycles and hydrological regimes (e.g., Mutch et al. 1993, Covington and Moore 1994). Shifts in forest structure and fuel loads also have led to feedbacks in fire regimes, and stand-destroying crown fires are today more prevalent in forests that experienced primarily surface fires (Covington and Moore 1994).

Here we describe historical patterns of fires and tree recruitment in stands of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and coast redwood (*Sequoia sempervirens*) at Point Reyes National Seashore on the central California coast. Changes in fire regimes and forest patterns over the past ca. 2 centuries were reconstructed from fire scars recorded in dendrochronologically-crossdated tree-ring series and forest stand ages. We concentrated our study in Douglas-fir and coast redwood forests within the Seashore boundaries in an attempt to obtain the longest possible records of both fire scars and age structures. Bishop pine (*Pinus muricata*) forests also are extensive at Point Reyes, but Bishop pine trees are generally too young (< 100 to 120 years old) for reconstruction of long-term fire history (Sugnet 1984, and other data from this study). Results from this study provide information on historical variability in fire frequency, timing, spatial patterning, and seasonality at Point Reyes that is necessary for

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management of vegetation and landscape patterns in this naturally-managed area (Morgan et al. 1994, Kaufmann et al. 1994).

Methods

Study Area

The Point Reyes Peninsula is separated from the California mainland by the San Andreas rift zone that forms the Olema Valley (Figure 1). Point Reyes National Seashore covers most of the Peninsula west from the Olema Valley. Inverness Ridge runs northwest to southeast down the length of the Peninsula (Figure 1) and reaches a maximum height of 428 m at Mt. Wittenberg. Inverness Ridge drops steeply to the east in a series of drainages while descending more gradually to the west in rolling hills and valleys to the Pacific Ocean. The Peninsula is underlain by relatively young granites and shales in contrast to the sedimentary substrates of the Franciscan complex of the adjacent mainland (Galloway 1977).

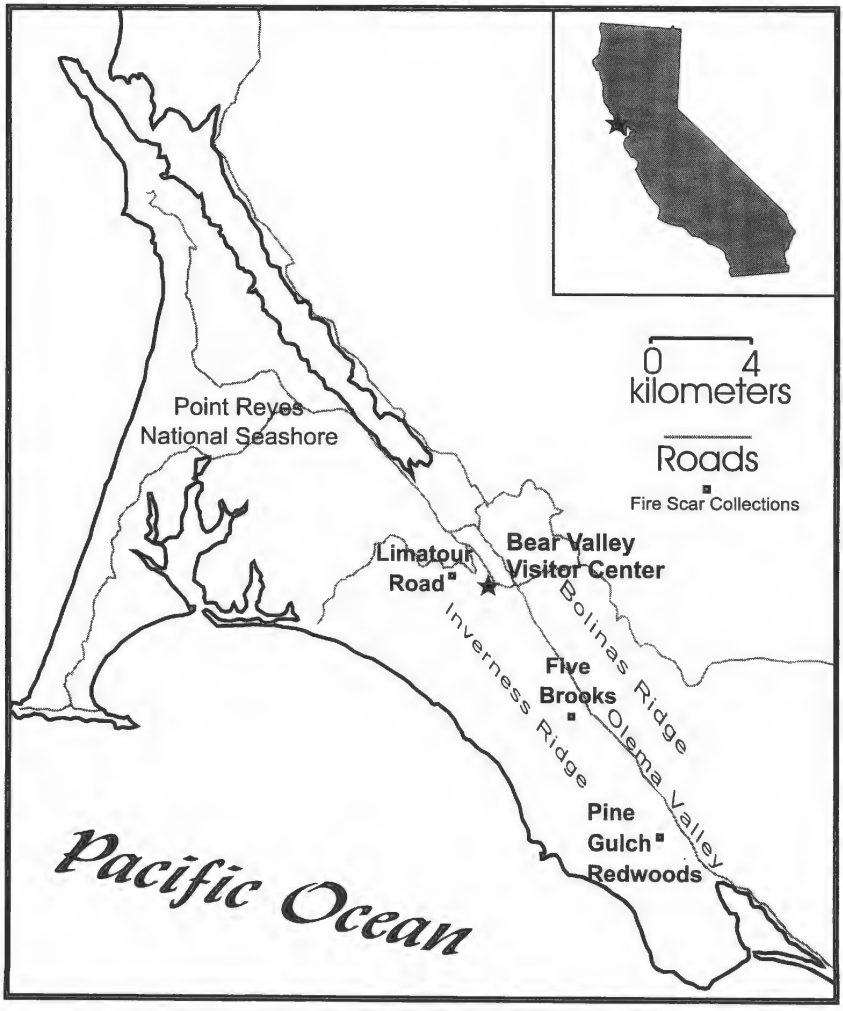

Figure 1. Locations of fire scar collections and place names mentioned in text.

A Mediterranean climate dominates, with wet winters and cool, dry summers. The coastal location and topography result in large variability in precipitation patterns. Average annual rainfall ranges from 460 mm on the western tip of the Peninsula to over 900 mm in the Olema Valley; over 80% falls from November through March. Coastal fogs during the summer contribute to increased soil moisture during otherwise dry summer months. Mean daily minimum and maximum temperatures range from 11° to 17°C in July and 6° to 13°C in January.

Inverness Ridge supports extensive coniferous forests while grasslands and coastal shrub or chaparral cover most of the rest of the Peninsula. Bishop pine forests dominate the north end of Inverness Ridge while predominately Douglas-fir forests are found in the south. Bishop pine is one of three species of relict closed-cone (serotinous) pine stands found in disjunct locations along the California coast (Duffield 1951, Critchfield 1966). Bishop pine generally occurs in pure, even-aged stands that established after crown fires (Wells 1962, Sugnet 1984). The Douglas-fir forest is usually considered to be a phase of the mixed evergreen forest of central California (Sawyer et al. 1977, Shuford and Timossi 1989) and often occurs with a sub-canopy layer of coast live oak (*Quercus agrifolia*) or California bay (*Umbellularia californica*) at Point Reyes. Most stands also have a dense shrub layer. A single stand of coast redwood is present on the southwest side of the Olema Valley in Pine Gulch (Galloway 1959), although more extensive stands are found on Bolinas Ridge (Figure 1) just to the east of the Seashore boundaries (Finney 1990). The coast redwood stands tend to have more open understories than the Douglas-fir forests, although they often have dense areas of shrubs, hardwoods, or occasionally abundant redwood regeneration from basal sprouts.

Human habitation of the Point Reyes area by the Coast Miwok began at least 5000 years ago (Treganza 1961, Duncan 1992). The earliest European contacts with the Coast Miwok were from Spanish and English voyages along the coast in the 16th century, the most famous of which was Sir Francis Drake in the *Golden Hinde* in 1579. Intensive Spanish influence in this area began in 1817 with establishment of a Franciscan mission at San Rafael, about 20 km southeast of the Seashore. After the Mexican revolution from Spain in 1821, the Point Reyes area was opened to land grant claims, the first of which was granted in 1836 in the Olema Valley (Toogood 1980). A long history of cattle and dairy ranching on the Peninsula began at that time (Livingston 1994, 1995). Cattle grazing is still present at Point Reyes, although grazing has not occurred within the forested areas since the 1960s and 1970s when the present Seashore boundaries were established.

Reconstruction of Fire History

Fire-scarred trees were opportunistically collected from three areas to reconstruct long-term patterns of surface fire events. Two areas, Limatour Ridge (LIM) and Five Brooks (5BR), are in the Douglas-fir forest and the third is in the coast redwood stand on the west side of Olema Valley (Pine Gulch Redwoods; PGR). In general, we searched for trees with sequences of fire scars that resulted from repeated fire events. These scar sequences are distinct from other injuries that may kill cambial tissues. We looked for fire-created "catfaces" from which we could remove partial circumference cross sections using chainsaws (Brown and Swetnam 1994). Catfaces are areas of open wood not covered with bark where cambial death occurred during fires or other injury events. However, owing to rapid growth exhibited by most trees at Point Reyes, living tissues on the margins of catfaces tended to grow over quickly and we found very few open catfaces on either living or remnant (logs or standing dead) trees. In an effort to obtain the most complete fire records for the Point Reyes area, we sampled extensively for hidden catfaces. This was accomplished on remnant trees by making "blind" cuts around a tree's base. Often we removed up to four partial circumference cross sections from different locations around a bole (Swetnam 1993, Brown and Swetnam 1994). All cross sections removed in this manner were from dead trees to minimize impacts on living trees in the National Seashore.

Tree-ring material was prepared and crossdated using standard dendrochronological methods (e.g., Swetnam et al. 1985). We developed a ring-width chronology from Point Reyes that aided in crossdating of remnant fire-scarred material. We assigned a position within the annual ring for fire scars or other injuries to assess possible seasonality of past fire events (Brown and Swetnam 1994). Dormant season scars (occurring between two rings) were assigned to the previous year (i.e.,

fall fires). Fire records from this area over the past century document that fires generally occurred from late August to November after radial growth had ceased (R. Moritz, Bolinas, California; unpublished data).

Composite fire chronologies were compiled for each cluster of fire-scarred trees using program FHX2 (Grissino-Mayer 1995). Fire frequency for each cluster was determined using three measures. Mean fire interval (MFI) is the average number of years between fire dates in a composite fire chronology and has been used widely to describe fire frequency (e.g., Romme 1980, Brown and Swetnam 1994, Grissino-Mayer 1995, Swetnam and Baisan 1996). Variability in fire intervals is described by the first standard deviation and range of intervals. Weibull median probability interval (WMPI) is the fire interval associated with the 50% exceedance probability of a modeled Weibull distribution of all fire intervals from a fire chronology and is considered to be a less-biased estimator of central tendencies in interval distribution (Grissino-Mayer 1995). Variability in fire data with the Weibull model is described by the 5% and 95% exceedance intervals (Grissino-Mayer 1995).

The third measure for fire frequency is determined as a regression slope fit through a cumulative sequence of fire dates (Brown et al. 1999). Piecewise linear regression procedures (Neter et al. 1989) were used to estimate the number of segments and break points in cumulative fire frequency through time (Brown et al. 1999).

Age Structure in Douglas-fir Stands

We examined maximum ages of overstory Douglas-fir trees to determine possible timing of establishment in the Douglas-fir forest on the east side of Inverness Ridge (Arno et al. 1995). Increment cores were collected using 50 cm increment borers from 10 dominant Douglas-fir trees in 24 plots located on a randomly-spaced grid laid out on the east side of Inverness Ridge. Total area covered by the grid was approximately 2000 ha. We measured diameter at breast height (DBH) of trees where cores did not reach pith or the vicinity of pith for later extrapolation of age. Larger-diameter (> 20 cm) sub-canopy hardwoods (oak and bay) were also sampled in plots where they occurred.

For ages of trees where sample cores did not reach pith, we estimated probable pith ages using either overlaid concentric circles or extrapolations based on measurements of ring widths. On cores where curvature of the inside rings was visible, we used overlaid circles to estimate the number of rings to possible pith locations (Arno et al. 1995). Pith ages were estimated to be from 1 to 22 rings with a majority (~75%) from 1 to 10 years from true pith locations using this method. For larger diameter trees, we used extrapolations of ring measurements to calculate number of rings to possible pith locations (Stephenson and Demetry 1995, Brown unpublished manuscript). Best-fit negative exponential or negative-slope linear equations were first determined for measured ring series from increment cores. These equations permitted us to account for wider rings towards tree centers. Equations were used to calculate backwards sums of ring widths until a probable radius was equaled. Radial distance was determined as 1/2 field-measured DBH for each tree and did not account for possible eccentricity in tree circumference. An average bark thickness of 3 cm was added to core lengths before extrapolations. The date of the inside ring at the point of equal radius was then used as pith age for the tree. Extrapolations from ring widths added from 15 to over 150 years to inside dates on increment cores from trees aged in this manner. We recognize that estimates of pith ages using this method are relatively crude but extrapolations based on ring widths were the only means available to estimate ages on trees that often exceeded 1 m and occasionally 2 m DBH (Stephenson and Demetry 1995).

Results and Discussion

Fire-Scar Records

Fire chronologies developed from fire-scarred trees at three sites on Inverness Ridge and in the Olema Valley are shown in Figure 2. Cross sections collected from Douglas-fir trees at Limatour Road (LIM) and Five Brooks (5BR) often recorded multiple fire scars (Figure 2). Fire-scarred cross sections from at least 20 other Douglas-fir trees were collected but could not be crossdated because of problems with either sample preservation or ring series that were too short to crossdate with the chronology for the area. Additionally,

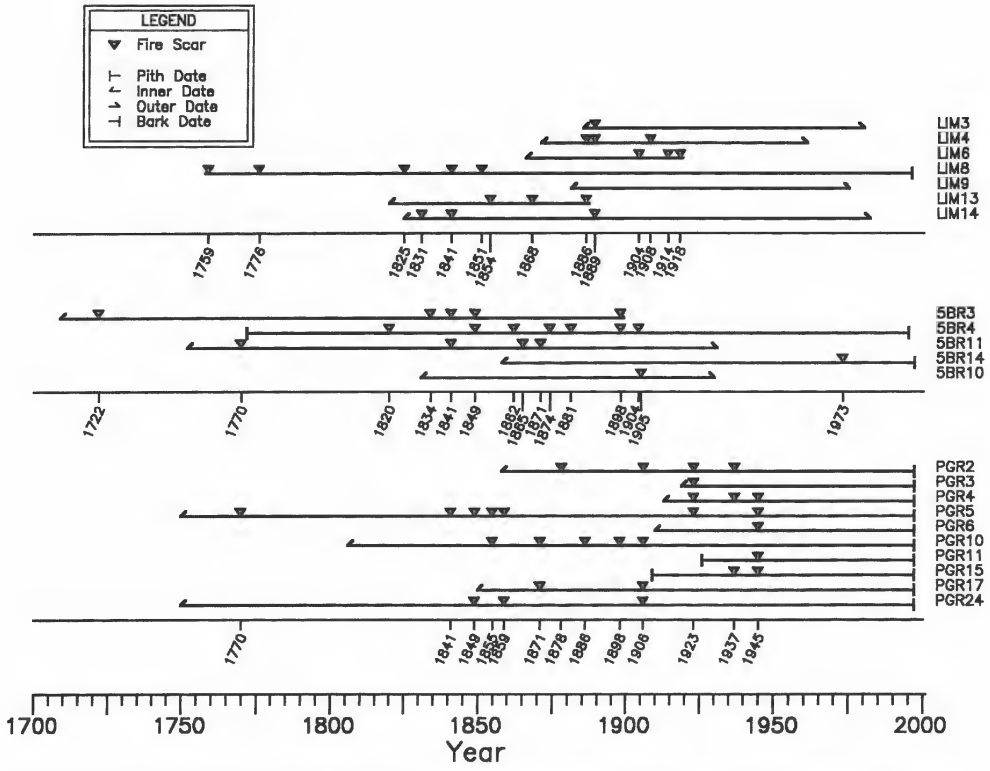

Figure 2. Fire chronologies for Point Reyes stands. Horizontal lines represent time spans of individual trees with inverted triangles at dates of fire scars.

ring widths in the Douglas-fir and coast redwood tended to be "complacent", with little variability in ring width, which made crossdating difficult on many trees. Most of the trees from sites 5BR and LIM were large diameter, 1 to 2 m DBH. However, because trees grow rapidly in this area (inside ring widths from 1 to 3 cm on many trees), most of the Douglas-fir sampled were not very old, and fire scar records did not extend much before the late 1700s. The oldest Douglas-fir tree (not fire-scarred) found in any of the areas sampled had an inside date of 1680.

Cross sections and increment cores were collected from 33 coast redwood trees at site PGR, although only 10 were successfully crossdated (Figure 2). The oldest trees on the northern California Coast are coast redwood, and they often contain long and well-preserved fire-scar records (Finney and Martin 1989, Finney 1990, Brown and Swetnam 1994). Large-diameter (> 2 m) stumps that grew prior to the 1800s were present at site PGR but were heavily decayed and burned from fires that occurred after this stand was logged. Toogood (1980) reports that logging of redwood stands in the lower Olema Valley and Bolinas Ridge began in the fall of 1849 and continued until 1858, with up to four lumber mills operating in the south end of the valley at the height of operations.

Coast redwood is an especially difficult species to crossdate because rings around tree circumferences are often incomplete (Finney and Martin 1989, Finney 1990, Brown and Swetnam 1994). We were not able to crossdate any of the pre-settlement trees from this stand. Most of the successfully crossdated tree were evidently basal sprouts that established after the original stand was logged or in response to fire events after logging (*sensu* Stuart 1987). In Figure 2, trees PGR 2 and 17 may have been sprouts that started after a fire in 1849, trees PGR 3, 4, 6, and 15 may

have sprouted in response to fire in 1906, and tree PGR 11 likely was a sprout that started in response to fire in 1923.

Fire scars were found on trees at two or three sites in the Olema Valley during several fire years (Figure 2). Fires were recorded at both sites 5BR and PGR during 1770, 1841, 1849, 1871, and 1898. Trees at these two sites were collected from near the bottom of Inverness Ridge in the Olema Valley where there are few topographic breaks to limit fire spread between the stands. However, with the exception of 1841, fires recorded by trees at LIM were not recorded at either of the other two sites (Figure 2). Trees from LIM were collected from drainages on Inverness Ridge above the Olema Valley, and it is likely that topographic breaks (ridges and valleys) limited fire spread from the valley bottom.

Only one fire scar was recorded in sites LIM and 5BR after the early 1900s, in 1973 (Figure 2). Three fires were recorded at PGR during the 20th century (Figure 2), all of which also were recorded in historic records (R. Moritz, unpublished data). Historic records used to document fire occurrences include all California Department of Forestry fire records for the Point Reyes area. A widespread fire in October, 1906, reportedly burned most of the Olema Valley and closely followed an extensive fire that burned most of Bolinas Ridge in 1904 (Marin Journal, October 25th, 1906). Widespread fires were recorded throughout the Point Reyes area in 1923 and reported to have burned over 40,000 acres (16,200 ha). Extensive fire in 1945 was reported to have burned over 18,000 acres (7300 ha), much of it on the west side of Bolinas Ridge. No fires have been recorded in the Pine Gulch redwoods stand since 1945. In addition, most fire scars were recorded late in the growing season or as dormant scars (Figure 3), which fits well with historic records that document the majority of fires occurred in the period from August to November.

Surface Fire Frequency

Measures of surface fire frequency for the Douglas-fir (5BR and LIM) and coast redwood (PGR) sites are in Table 1. A period of analysis for fire frequency was determined for each site based upon piecewise regressions of cumulative fire dates (Figure 4). In Figure 4, all fire dates are plotted as cumulative data. However, dates before the early to middle 1800s from each site do not fit

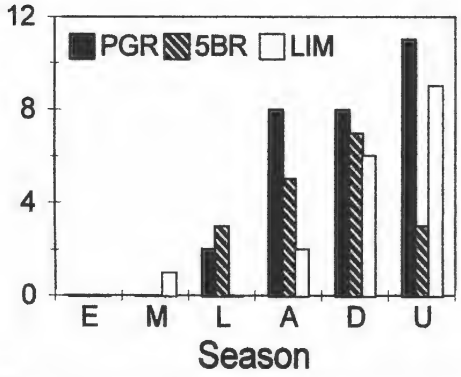

Figure 3. Positions of fire scars within annual rings for three sites at Point Reyes. E: within the first third of the earlywood band; M: middle third of earlywood; L: last third of earlywood; A: in the latewood band; D: dormant season; U: unknown position due to narrowness of rings, ring damage, or other factors. Dormant season scars were dated to the earlier year.

longer-term trends in cumulative events. It is probable that fire dates are missing from the fire scar records before this period. Fire frequency at site PGR was broken into two segments based on results from piecewise regression procedures. Regression slopes before and after 1906 were determined to be significantly different ($P > 0.10$) based on analysis of variance of regression results.

Measures of fire frequency from the early 1800s to early 1900s are consistent for all three stands (Table 1). Mean fire intervals (MFIs) ranged from 7.7 to 8.5 yrs while Weibull median probability intervals were slightly lower reflecting the generally positive skews in interval distributions. Variability in intervals as reflected by standard deviations, ranges, and Weibull 5% and 95% probability intervals also were consistent between stands. MFIs found by this study fit well with reconstructed fire frequency from coast redwood stands on Bolinas Ridge (Finney 1990). Finney found fire frequencies between 1850 and 1900 ranged from 6 to 33 years, with a mean of 14 years.

In addition to crossdated fire events on living coast redwood trees at site PGR, we collected fire scar sequences from five pre-settlement coast redwood stumps. Point fire intervals (i.e., average fire-scar intervals from individual trees) were calculated from these five trees using ring counts between fire scars (Table 2). These sequences of fire scars may be incomplete because fire scars

TABLE 1. Fire frequencies for Point Reyes sites. Fire frequency is calculated using intervals between all fire dates at each site for the period of analysis.

Site	Period of analysis	No. of intervals	MFI (± SD)[1]	Range of intervals [2]	WMPI [3]	5% to 95% prob. inter. [4]	Fire frequency (from fig. 4)[5]
PGR	1841 to 1906	8	8.1 ± 2.7	4 to 12	8.2	4.0 to 12.3	0.122
PGR	1906 to 1945	3	13.0 ± 4.6	8 to 17	13.2	6.0 to 22.7	0.075
PGR	1841 to 1945	11	9.5 ± 3.8	4 to 17	9.4	4.1 to 15.0	
5BR	1820 to 1905	11	7.7 ± 5.0	1 to 17	6.9	1.3 to 17.6	0.130
LIM	1825 to 1918	11	8.5 ± 5.3	3 to 18	7.8	2.1 to 16.0	0.107

[1] Mean fire interval and standard deviation of all intervals in composite fire chronology in years.

[2] In years.

[3] Weibull median (50% exceedance) probability interval in years.

[4] Weibull 5% and 95% exceedance probability intervals in years.

[5] Piecewise regression slopes calculated from cumulative fire dates (number of fires year^{-1}).

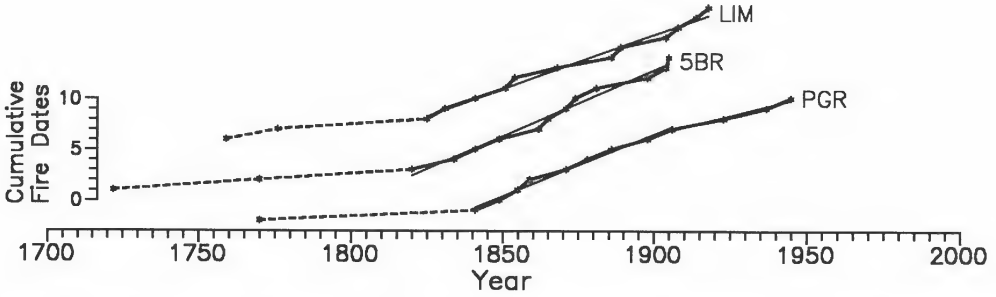

Figure 4. Fire frequency in stands determined from linear regressions fit through cumulative fire dates. Dashed lines are between fire dates not used in periods of analysis for fire frequency (see text). There is a significant difference in regression ($P > 0.10$) before and after 1906 at site PGR.

may not have been recorded in every fire event or fire scars may have been eroded or lost from a scar record. Missing rings between fire scars can be a common occurrence in coast redwood (Brown and Swetnam 1994) and may also bias mean intervals. However, averaging of fire intervals resulted in close agreement of point intervals between trees (Table 2). Unfortunately, without crossdated ring sequences, it is unknown what time period these fire frequencies may represent, only that they are from some time before logging of the stand in the 1850s. These "floating" fire scar sequences at least suggest that there have been relatively high fire frequencies in the Olema Valley during periods before the 19th century. Point fire intervals of 8 to 12 years on the PGR samples (Table 2) fit well with roughly-dated MFIs that ranged from 8 to 20 years from 1450 to 1850 found by Finney (1990) in coast redwood stands on Bolinas Ridge.

TABLE 2. Number of years, means and standard errors (in years) between fire scars in sequences recorded on undated pre-settlement coast redwood trees from Pine Gulch redwoods stand.

tree: intervals	mean ± SE.
PGR 18: 11, 16, 6	11.0 ± 5.0
PGR 22: 6, 11, 18, 5, 8, 11, 12	8.7 ± 5.5
PGR 28: 3, 11, 13, 6, 8, 16, 4, 7, 10, 3	8.1 ± 4.4
PGR 29: 7, 17	12.0 ± 7.1
PGR 30: 6, 6, 7, 8, 15	8.4 ± 3.8

Age Structure in Douglas-fir Stands

Ages of overstory Douglas-fir trees from 24 plots in the Bear Valley area of Limatour Ridge document an apparently multiaged forest with no evidence of even-aged forest structure over large areas (Figure 5). Although extrapolated pith ages based on ring measurements are only crude estimations

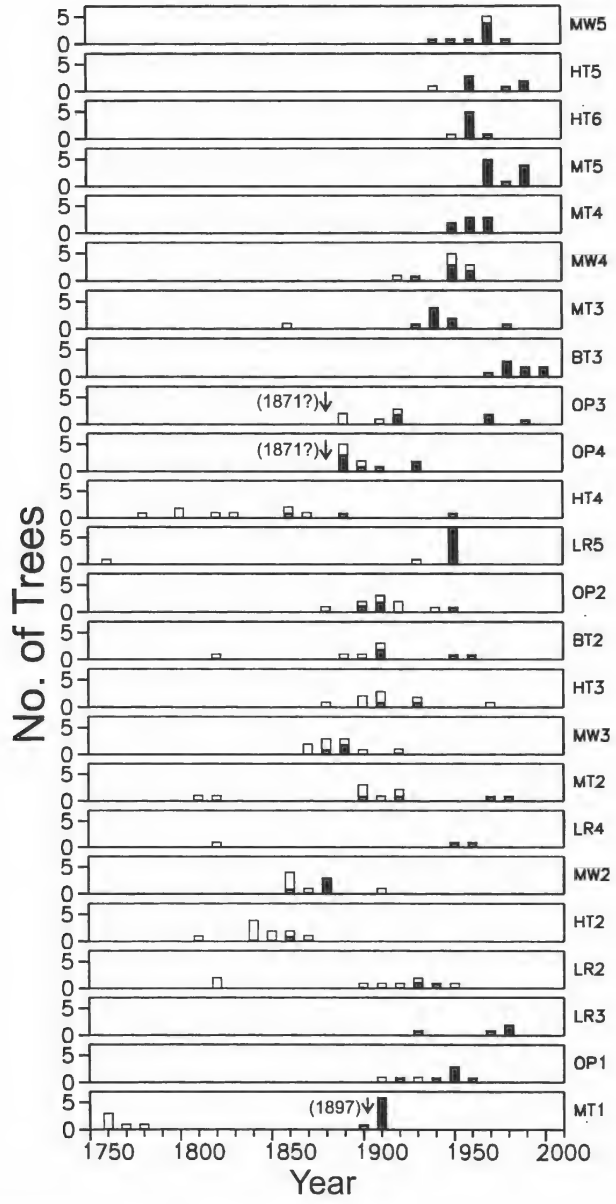

Figure 5. Estimated pith dates on overstory Douglas-fir trees from 24 plots in Bear Valley area of Inverness Ridge. Plots are arranged from bottom to top based on elevation from the bottom of Olema Valley to the top of Inverness Ridge. Solid portions of histograms are numbers of center dates determined from overlaid concentric circles where inside curvature of rings was visible on increment cores. Estimated number of rings from inside of core to probable piths ranged from 1 to 22, with a majority ≤10 rings. Open portions of histograms are numbers of pith dates determined from radial extrapolations of ring widths (see text). These dates may have larger errors owing to extrapolation procedure. Arrows mark possible stand-replacing fire dates in plots.

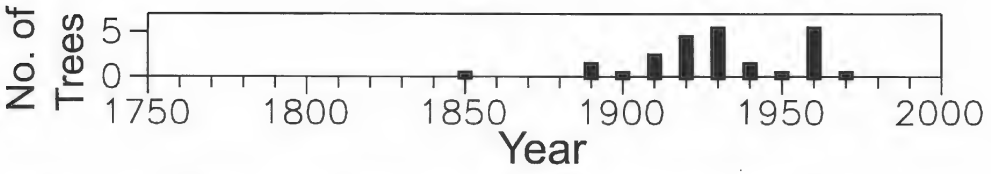

Figure 6. Numbers of understory oak and bay trees by center dates from all plots in the Bear Valley area.

of true ages, there is no clustering of dates over the approximately 2000 ha area where trees were sampled. Trees were young for the most part, with few trees in any plot over 200 years old. Ages of trees from plots near the top of Inverness Ridge were especially young (Figure 5). Several of the individual stands seem to have a maximum age cohort that may be related to stand-destroying events, such as catastrophic fires, logging, or unknown disturbances. The 1871 fire year was recorded as fire scars at sites 5BR and LIM, and trees at two plots (OP3 and OP4) did not have any trees that dated from before this year. A number of trees established at these two plots beginning in the late 1870s. Only 2 fire-scar dates were sampled on any trees in the plots. A fire scar was recorded on a single tree in plot BT2 in 1927. In plot MT1, fire scars were recorded on 2 trees in 1897. Five trees in the stand established in the early 1900s.

Understory hardwoods (bays and oaks) were younger than overstory Douglas-fir in all stands where hardwoods were collected (Figure 6). Abundant sub-canopy hardwood regeneration and little to no Douglas-fir regeneration was seen in many of the Douglas-fir stands. These patterns suggests that in the absence of Douglas-fir regeneration, hardwood trees may eventually replace Douglas-fir.

Implications of the Fire History for Vegetation Dynamics and Landscape Patterning

Results from this study document characteristics of the fire regime in Douglas-fir and coast redwood stands in the Olema Valley and on Inverness Ridge during the period from the middle 1800s to early 1900s. Average intervals between fires were similar between stands and ranged from 8 to 9 yrs. Fires were apparently variable in size, with most fire years recorded at only one site and fewer fires recorded at two or very rarely three sites (Figure 2). Historic records also document highly variable fire sizes from local stands to extensive landscape-scale events.

Longer-term fire history data from the Point Reyes area document relatively high surface fire frequency before the early 1800s. Floating fire scar sequences from pre-settlement coast redwood stumps in site PGR document point MFIs of 8 to 12 yrs prior to the middle 1800s (Table 2). Fire scars from Finney's (1990) study in coast redwood stands on Bolinas Ridge document comparable high fire frequency in this area at least back to the middle 1400s. The presence of charcoal layers in sediments from lakes in the south end of the Point Reyes Peninsula further support the regular occurrence of fire in forests of this area over the past several centuries (Russell 1983, Duncan 1992).

Surface fires ceased for the most part at all sites in the early to middle 20th century, with only one fire scar recorded at any stand after 1945 (Figure 2). Shifts in fire frequency from pre-settlement or early settlement periods to recent decades have important implications for assessing possible changes in landscape patterning and composition and structure of present-day forest stands. Frequent surface fires would have tended to maintain more open stands by killing young trees before they could become established in the overstory. Frequent fires on forest margins also would have tended to maintain the position of forest/grassland or forest/shrubland ecotones. Historical references and records of vegetation patterns on the California coast in the vicinity of Point Reyes document less forest on the coastal hills than at present. Viscaíno in 1602 described the coastal ranges north of Point Reyes as "places of *sierra* [hills] bare to the sea" (Aker 1965; quoted in Duncan 1992:213). In 1792, Vancouver noted that, "the verdure of the plain continued to a considerable height up the sides of the hills, the summits of which...one could see produced a few trees" (Vancouver 1967:10; Wilbur 1953:1). Von Kotzebue during an expedition in the 1810s

described the Point Reyes area as "barren with few scattered trees on the higher elevations and patches of dwarf shrubs in the valleys" (Von Kotzebue 1967:48; quoted in Duncan 1992:242). Topographic and vegetation maps of the coast and a mile inland produced by the US Coast Survey from 1859 to 1862 show forested or shrub vegetation primarily in drainages on the east and west sides of Inverness Ridge but not on the ridge itself (maps on file at Point Reyes National Seashore). Historical photographs of Inverness Ridge and the Olema Valley taken in the late 19th and early 20th centuries (Livingston 1994, 1995) also document open hillsides and more extensive areas of grasslands prior to the middle 20th century than are present in these same areas today.

Age structures in Douglas-fir plots from Limatour Ridge show that large numbers of trees have established in these stands since the early 1900s (Figure 5). Most of the hardwoods in the stands also established after the early 1900s (Figure 6). Wills and Stuart (1994) found similar patterns of heavy recent regeneration in Douglas-fir/hardwood stands on the Klamath National Forest in northern California in the absence of surface fires. Age structures in stands from near the top of Inverness Ridge document encroachment of the Douglas-fir forest into these areas (Figure 5). Almost all trees from the plots near the top of the ridge established after the early to middle 1900s, and confirm shifts in landscape patterns of forest and grass or shrub communities.

Patterns in the fire regime at Point Reyes were most likely influenced by human activities. It is probable that some (if not most) of the fire events recorded by trees in Figure 2 were the result of human ignitions. References to Native American burning practices are extensive (e.g., Boyd 1999), and the Coast Miwok that occupied this area prior to the nineteenth century were known to have set fires for clearing brush, hunting, or accidentally (Treganza 1961, Duncan 1992). Intensive non-Native American settlement began in the early to middle 1800s. References in Livingston (1994, 1995) suggest that clearing of brush from grasslands was a frequent occupation of the early ranchers and dairy farmers on the Peninsula. While not often stated explicitly, setting fires to burn off the land would have been a possible means for clearing of brush.

The probable role of humans in historical fire regimes at Point Reyes leads to questions concerning the appropriate approach to management of ecosystems on the Peninsula. In the absence of human ignitions, it is likely that fires would not have been as common. Lightning ignitions are rare for this area, especially during the later summer/early fall period when grasses and herbaceous fuels cure and the majority of fires occurred. However, regardless of the source of ignitions in pre-settlement or early settlement fire regimes, forests of the Point Reyes Peninsula are not burning today with nearly the frequency they did in the past. Shifts from understory to overstory dominance, increases in fuel loads, and changes in forest structure (i.e., increases in "ladder fuels") may lead to increased incidence of overstory, stand-destroying fires that have been documented in other forests that experienced frequent surface fires prior to widespread non-Native American settlement (e.g., Covington et al. 1994). Conversion of grasslands to forest also will continue in the absence of fires. In addition, fires influence many ecosystem-level functions, such as nutrient cycling and energy flows, by rapid chemical and physical changes in both living and dead biomass. The loss of surface fires from forests of the Point Reyes Peninsula most likely has had and will continue to have cascading effects on landscape patterns and ecosystem processes (e.g., Covington and Moore 1994).

Acknowledgements

Will Joaquin and Tad Gerace assisted with field collections. Two anonymous reviewers provided valuable comments on the manuscript. Ray Moritz provided data on recent fire history in the Point Reyes area. We thank Point Reyes National Seashore personnel for assistance with field collections and logistics. This research was supported by the US Department of the Interior, Point Reyes National Seashore, through Cooperative Agreement No. 1443-CA-8530-97-010.

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Received 24 February 1999
Accepted for publication 22 June 1999

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Mycorrhizae and Fine Root Dynamics of *Centaurea maculosa* and Native Bunchgrasses in Western Montana

Abstract

Centaurea maculosa is an invasive exotic pest plant of intermountain grasslands of the western United States. We investigated whether there were differences in fine root and mycorrhizal development between the exotic forb *C. maculosa* and two native grasses, since these are factors known to influence competitive ability of plants. We measured colonization by arbuscular mycorrhizal (AM) fungi of the native bunch grasses *Pseudoroegnaria spicata* and *Festuca idahoensis*, and *C. maculosa*, and used root periscopes to investigate fine root patterns of *P. spicata* and *C. maculosa*. AM fungal colonization of the exotic was similar to *F. idahoensis* in 1995 (43.6% vs. 44.7%), and was higher than *P. spicata* in 1995 and 1996 (43.6% vs. 26.9%, and 55.4% vs. 15.6%). Colonization of the grasses was not affected by the presence of *C. maculosa*. Fine roots of *C. maculosa* developed earlier, with a higher proportion of deep roots than *P. spicata*. Thirty nine per cent of *C. maculosa* roots, but only 25% of *P. spicata* roots, were deeper than 30 cm. Early and deep root development and extensive mycorrhizal colonization in the field may contribute to competitive dominance of *C. maculosa*.

Introduction

Spotted knapweed (*Centaurea maculosa* Lam.) is one of the most destructive exotic pest plants in North America, and can establish nearly monocultural stands in previously diverse intermountain prairie communities. Invasions are influenced by both the abiotic conditions of the new range and by biological traits of the invading species; insight into biology of invasive plants can contribute to our understanding of invasions. With as much as 50-80% of net productivity in prairie communities being belowground (Caldwell 1979), it is important to understand belowground interactions, and their role in the competitive effects of exotic species (Harris 1967, D'Antonio and Mahall 1991, Goodwin 1992, Holmes and Rice 1996). Spatial and temporal rooting patterns, and mycorrhizal associations are two major factors influencing belowground competition. Occupation of soil space is a primary determinant of below ground competitive ability, and can be quantified as root density, vertical distribution, and phenology (Casper and Jackson 1997, Schenk et al. *in press*). High root density enhances the exploitation of patchy resources (Jackson and Caldwell 1989, Callaway 1990, Caldwell et al. 1991, Jackson et al. 1990, Caldwell et al. 1996), and can exclude neighbor root systems. This can in turn produce strong competitive effects on neighbors (Callaway et al. 1991, Schenk et al. *in press*). The phenology of root growth may contribute to preemptive occupation of space, and the ability of plants to respond to ephemeral resource availability (Harris 1967, Jackson and Caldwell 1989, Holmes and Rice 1996, Casper and Jackson 1997).

For many species, the performance of fine roots is closely tied to the development of mycorrhizal associations. Arbuscular mycorrhizal (AM) fungi are common root symbionts that can improve plant mineral status (Allen and Allen 1990, Brundrett 1991) and influence the outcome of competitive interactions among host species. Plant response to AM fungi depends on resource availability, species-specific differences in mycorrhizal dependence (Hetrick et al. 1989, Allen et al. 1984, 1988, Grime et al. 1987, Allen and Allen 1990, Hartnett et al. 1993, Zobel and Moora 1995, Moora and Zobel 1996), and the species composition of the AM fungal community (Allen and Allen 1988, Johnson 1993, Francis and Read 1994, Bever et al. 1996). AM fungi have been shown to influence competition between exotic and native species (Goodwin 1992, Marler et al. 1999) but little is known about the impact of invasions on native mycorrhizae (but see Johnson and Wedin 1997).

Fine root dynamics and mycorrhizal colonization are often interrelated in their effects. For

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example, rooting patterns can be more plastic if plants are facultatively mycorrhizal, and plants with more fibrous root systems tend to be less dependent on mycorrhizae (Hetrick 1991, Hetrick et al 1992, Muthukumar et al 1996). Timing of root growth and level of colonization by AM fungi have also been shown to influence the effectiveness of root boring insects used as biological control agents on the noxious weed *Centaurea diffusa* Lam. (diffuse knapweed) (Harris and Clapperton 1997). However, few field studies have addressed the dynamics of AM fungi and rooting patterns for the same species in the same habitat.

We investigated the dynamics of fine roots and mycorrhizae in the field for the noxious weed *Centaurea maculosa* and native bunchgrasses, with the objective of describing patterns in and relationships between their development. We compared fine root density and phenology at four depths between *C. maculosa* and *Pseudoroegnaria spicata* (Pursh) A. Löve (bluebunch wheatgrass, syn. *Agropyron spicatum*), and compared the extent and phenology of mycorrhizal colonization of *C. maculosa*, *P. spicata* and *Festuca idahoensis* Elmer (Idaho fescue).

Methods

Study Areas

We quantified root distributions and phenologies for *C. maculosa* and *P. spicata*, and mycorrhizal colonization for *C. maculosa*, *P. spicata* and *F. idahoensis* occurring on a southwest slope of Mount Sentinel (elevation 1294m), adjacent to the University of Montana campus in Missoula in 1995. Mycorrhizal colonization of *C. maculosa* and *P. spicata* was also measured at a site 4.2 km east of Hamilton, Montana (elevation 1334 m, approximately 80.5 km south of Missoula) in 1996. Both sites have been invaded by other exotic species, including *Linaria dalmatica* (L.) Mill. (Dalmatian toadflax), *Euphorbia esula* L. (leafy spurge), and *Bromus tectorum* L. (cheatgrass), but retain remnant patches of native prairie in good condition (i.e. very few exotic plants).

Root Density, Depth, and Phenology

In April 1995, we inserted 60-cm-long plexiglass tubes under 10 large *C. maculosa* plants and 10 large *P. spicata* plants as permanent mini-rhizotrons for root viewing. Since *C. maculosa* has been shown to have allelopathic effects on neighbors (Ridenour 1995), we placed periscope tubes beneath *P. spicata* individuals growing without *C. maculosa* nearby (>5m). The periscope tubes were inserted at a 15-degree angle from vertical to enhance root contact with the transparent walls. Sections were marked at fifteen-cm intervals on the wall of the tube, and weekly or bi-weekly measurements were taken with a root periscope (Richards 1984) beginning on April 13, 1995 and ending on September 28, 1995. On each sampling date, all white tips of fine roots were counted in each of the following depth categories: 0-15 cm, 15-30 cm, 30-45 cm and 45-60 cm along the tube surface. We counted only roots with white growing tips because they were the most likely to be growing and absorbing resources.

Sampling and scoring of roots for mycorrhizal colonization.

We sampled AM fungal colonization of grasses and *C. maculosa* that were isolated and that were intermixed, providing an estimate of plant community effects on mycorrhizal colonization. At the Missoula and Hamilton sites, we identified communities that were 1) "native," i.e. 0-10% *C. maculosa*; 2) "mixed," 10-25% *C. maculosa*; or 3) "exotic," with more than 25% cover by *C. maculosa*. These categories are merely descriptive. We collected roots in the top 15-cm of soil from 15 randomly selected individuals of each grass species from native and mixed communities. While mycorrhizae can be found at depths greater than 15 cm, they often decline sharply with depth (Cooke et al. 1993, Al-Agely and Reeves 1995, Barnola and Montilla 1997, Ingleby et al. 1997), so we sampled in the top 15 cm for consistency. Samples were taken with a trowel, and roots were taken attached to the culms, so root identification would be possible. We collected at least 15 *C. maculosa* individuals from the mixed and exotic communities. Sampling was repeated at six-week intervals (mid-May, early July, and mid-August) over the summers.

Roots were washed in the lab, then cleared in 2.5% KOH for 48 hours, acidified in 5% HCl for 12 hours, and stained in trypan blue for 12 hours. All steps were done at room temperature. Vesicles, arbuscules and hyphae were scored using a magnified intersection method (McGonigle et al. 1990). For each individual we scored four transects

through 36 one-cm root sections for a total of approximately 144 random intersections per individual.

Statistical Analyses.

Repeated measures ANOVA was used to test for differences in root density between the two species and the four depths over the 1995-growing season. Fine root data was normally distributed and was not transformed.

Data for total colonization and vesicle density in 1995 (Missoula site) were transformed with arcsine of square root functions prior to analysis. These data were normal for the 1996 season (Hamilton site) and were not transformed. Arbuscule data in both years were not normal even after transformation, so the non-parametric Mann-Whitney U-test for rank was used for analysis. For *C. maculosa*, a two-way analysis of variance was used to determine the effect of community type (exotic or mixed) and sampling date on total colonization and vesicle density. For *P. spicata* and *F. idahoensis*, a separate three-way analysis of variance was used to test the effect of host species, community (native or mixed) and sampling date on total colonization and vesicle colonization. The three species could not be analyzed in the same ANOVA since the treatments within community type were different for the grasses and *C. maculosa*. Comparisons between total colonization and vesicle density of *C. maculosa* and the grass species were made with t-tests. Comparisons of arbuscule density between species and community types were made with the Mann Whitney U-test for rank.

Results

Rooting patterns.

Averaged over all depths and sampling dates, *C. maculosa* and *P. spicata* did not differ in fine root density (Table 1, P=0.519). However, there was a significant difference in root density at the different depths (P<0.001), and the interaction term for species by depth was significant (P<0.001), indicating root growth differed with depth for the two species. *Centaurea maculosa* developed fine roots earlier than *P. spicata* at all root depths (Figure 1), and its roots were more abundant at the two lower soil depths than those of the bunchgrass. Over the entire measurement period, *C. maculosa* had 39% of its total roots in the lower 30 cm of soil, while *P. spicata* had 24% at that depth. *Centaurea maculosa* had 4 times as many roots as *P. spicata* in the 45-60 cm layer of soil (Figure 1).

TABLE 1. Repeated measures ANOVA for differences in rooting distribution between *C. maculosa* and *P. spicata* over time.

Source	Type 3 Sum of Squares	df	Mean Squares	F	Sig.
Intercept	372171	1	372171	310.80	0.00
Species	504.34	1	504.34	0.42	0.52
Depth	60037.10	3	20012.40	16.71	0.00
Species*depth	11839.80	3	3946.604	3.30	0.03
Error	81426.800	68	1197.453		

At shallow depths (0-15 cm), phenological fluctuations in root density of the two species were correlated (r=0.69), suggesting that fine roots of both species were responding similarly to environmental conditions (e.g. soil moisture or temperature) over the growing season. No significant correlation was observed for roots at the 45-60 cm profile (r=0.14) indicating that root dynamics were less affected by seasonal changes, and were largely driven by inherent species-specific morphology and development.

Mycorrhizal colonization

Total mycorrhizal colonization did not differ between *C. maculosa* and *F. idahoensis*, but both of these species had higher total colonization than *P. spicata* (Table 2). At both sites, vesicle density was significantly higher in *C. maculosa* roots than in either grass species (Table 2). At the Missoula site, *F. idahoensis* had the highest arbuscule density, while *C. maculosa* and *P. spicata* did not differ significantly. At the Hamilton site, *C. maculosa* had significantly more arbuscules than *P. spicata* (Table 2).

Timing of sampling had a significant effect on total AM colonization of *C. maculosa* in both years (1995 P_{date}=0.001, 1996 P_{date}=0.005). Total colonization of *C. maculosa* was higher in July and August than in May at the Missoula site, and peaked in July at the Hamilton site (Figure 2). The analysis of variance did not indicate an effect of sampling date on total colonization of the grasses in 1995 (P_{date}=0.086), although post hoc

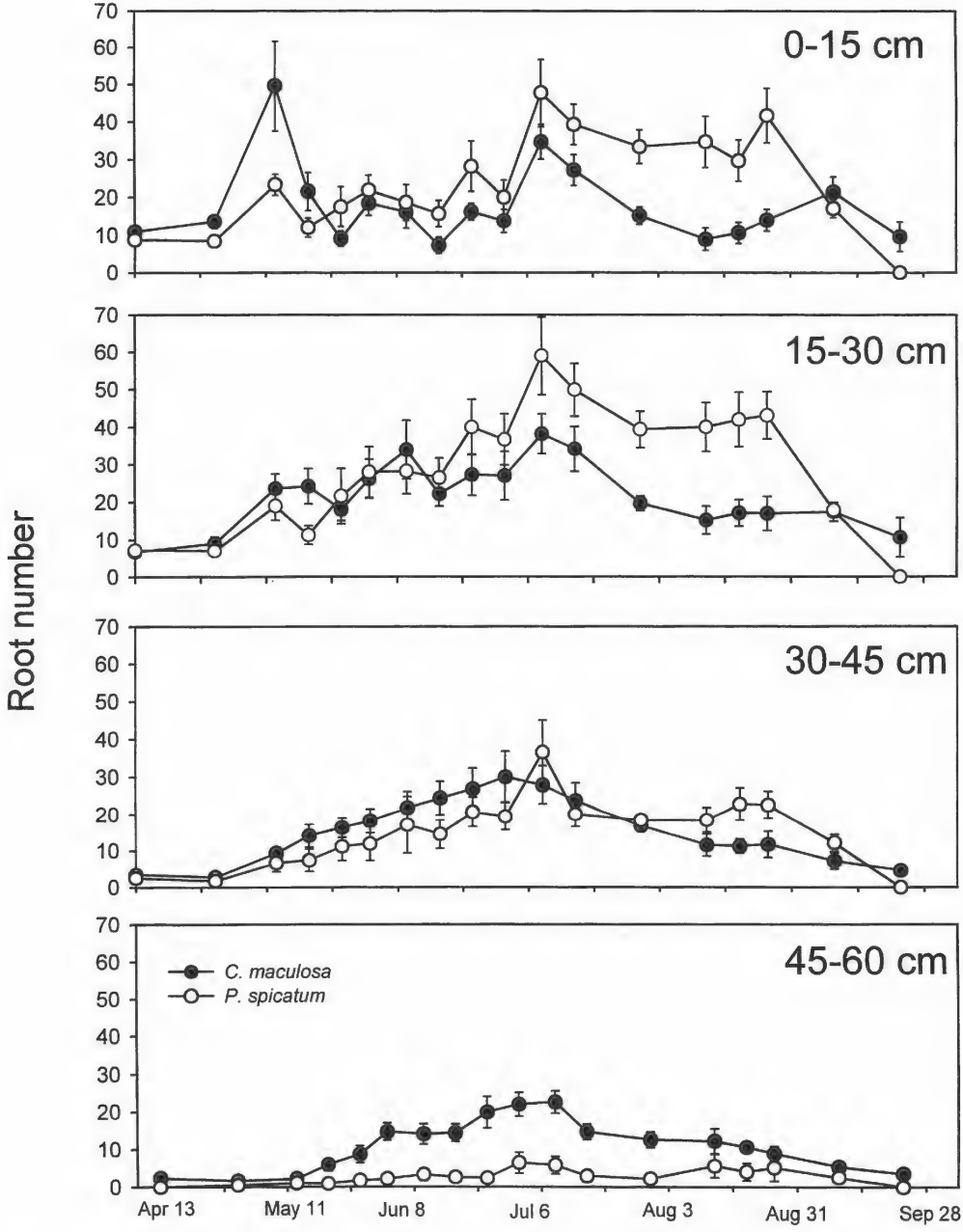

Figure 1. Number of fine roots of *C. maculosa* and *P. spicata* at each depth in 1995. Error bars represent one standard error of the mean.

TABLE 2. Comparisons of mean AM colonization among species. Transformed values for vesicle density and total colonization were compared with t-tests; actual means are given. Arbuscule density was compared with the Mann-Whitney U test for rank. Values in a column at each site that are followed by different letters are significant at P<0.05. Values in parentheses are the standard error of the mean.

	Total colonization[1]	Vesicle colonization[1]	Arbuscule colonization
Missoula site[1]	mean (s.e.)	Mean (s.e.)	Mean (s.e.)
P. spicata	0.269(0.018)a	0.021(0.004)a	0.008 (.002) a
F. idahoensis	0.447(0.021)b	0.025(0.003)b	0.043 (.009) b
C. maculosa	0.436(0.023)b	0.045(0.006)c	0.004 (.001) a
Hamilton site			
P. spicata	0.156 (0.013) a	0.011 (.002) a	.002 (.001) a
C. maculosa	0.554 (0.021)b	0.038 (.004) b	.006 (.001) b

[1]At the Missoula site, total colonization and vesicle density were transformed with arcsine of the square root function. At the Hamilton site, total colonization and vesicle density were normally distributed.

analysis suggests that total colonization of *P. spicata* decreased over the growing season (Figure 2). However, in 1996 sampling date did influence total colonization of *P. spicata* (P_{date}<0.0001), which increased over the season.

Vesicle colonization of *C. maculosa* roots significantly increased over the season in 1995 (P_{date}=0.036) but there was no effect of date on vesicle colonization at the Hamilton site (P_{date}=0.148). There was no significant effect of date on vesicle density in grass roots in either year. Community type did not affect total AMF colonization of any species. However, vesicle colonization of *C. maculosa* differed between community types in both years (1995 $P_{community}$=0.015, 1996 $P_{community}$<0.01), but in different directions each year: colonization was higher in the mixed community in 1995, but higher in the exotic community in 1996. This is further compounded by the difference in sites each year.

Discussion

Our comparison of root phenology and mycorrhizal colonization suggests several mechanisms that may contribute to competitive dominance of *C. maculosa. Centaurea maculosa* developed roots earlier at all depths, and produced more roots throughout the growing season at the 45 – 60 cm depths, than the native *P. spicata.* Such rapid acquisition of space is important for competitive dominance (Casper and Jackson 1998, Schenk et al. *in press*). Ability to occupy belowground space more rapidly than natives may allow *C. maculosa* to preempt available resources, as has been shown for other invasive species (Harris 1967, Sheley et al. 1993). Earlier growth and deeper rooting distribution suggests that the invader may have access to a wider range of soil resources than *P. spicata*. The fact that there was no effect of community type on AM fungal colonization indicates that interference with native mycorrhizae is not a likely mechanism of competitive dominance.

Mycorrhizal colonization levels were consistently higher for *C. maculosa* than *P. spicata*. Since we observed AM colonization at two sites in separate years, it is impossible to make strong conclusions about phenological differences between species in vesicles or arbuscules. These are known to vary with differences in soil types (Johnson-Green et al. 1994, Klironomos 1995) and between years for reasons that are not understood (Allen et al. 1989, Sanders and Fitter 1992). Levels of total mycorrhizal colonization were comparable between *C. maculosa* and *F. idahoensis*, and were higher at both sites in *C. maculosa* than *P. spicata.* AM fungi strongly enhance *C. maculosa*'s competitive dominance over *F. idahoensis* in greenhouse experiments (Marler et al. 1999), so the high level of colonization we found allows for the possibility of similar mechanisms functioning in the field. Also, higher levels of mycorrhizal colonization may increase phosphorus and nitrogen uptake (Hoffman and Mitchell 1985, Allen and Allen 1990) over *P. spicata*.

Early in the season, *C. maculosa* generated more fine roots with a lower level of AM colonization, while later in the season, colonization levels increased while fine root production decreased. It

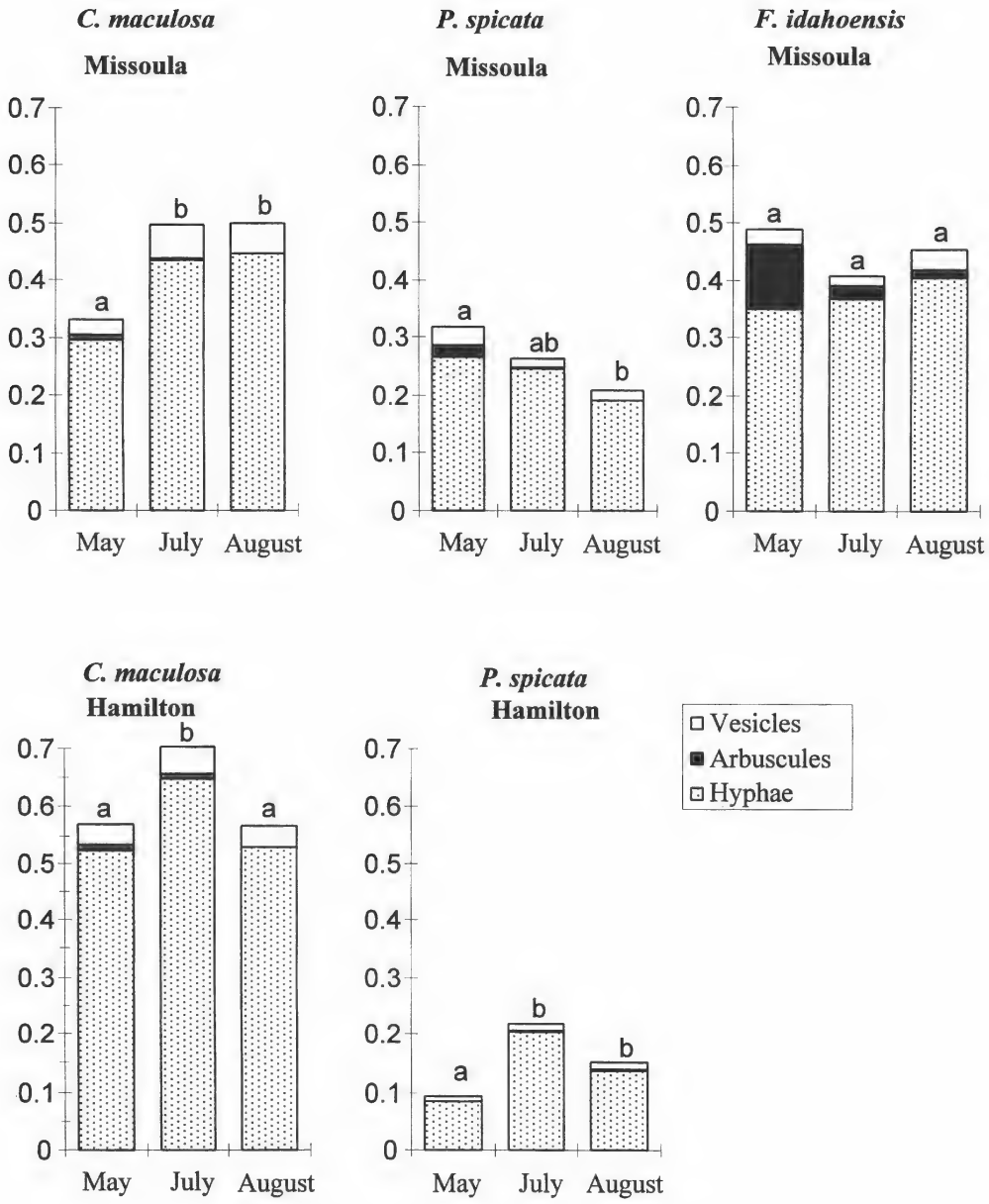

Figure 2. Proportion of roots colonized by arbuscular mycorrhizal fungi in 1995 (Missoula) and 1996 (Hamilton).

is noteworthy that *C. maculosa* allocated more carbon to roots at deeper levels, while maintaining mycorrhizal associations at shallow depths.

Our data support a growing body of work that suggests below ground processes are important to the invasiveness of *Centaurea maculosa*. By developing fine root systems more rapidly and in deeper soil horizons, and by utilizing *in situ* mycorrhizal communities, this exotic invader may gain competitive advantages over native species. This study should be considered preliminary, and more detailed studies encompassing multiple years are warranted to further investigate these relationships.

Acknowledgements

This research was funded by USFS INT-95126 RJVA to MJM and NSF EPSCoR grant OSR-955450. We thank Erik Aschehoug, TJ Fontaine, Trevor Laboski, Jodee Smith and Lauren Quinn, for field and lab assistance. David Schmetterling and Anna Sala made many helpful comments on the manuscript.

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Received 27 October 1998
Accepted for publication 12 June 1999

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Blister Rust Testing in British Columbia: Choosing Inoculum Sources and a Screening Site

Abstract

In order to test for possible geographic variants in white pine blister rust (*Cronartium ribicola* J.C. Fisch.), four rust sources from British Columbia (BC), Canada were cultivated on *Ribes* spp. and used to inoculate sets of 2-year-old seedling progeny of 24 parents of western white pine (*Pinus monticola* D. Don). The six parents from Coastal United States possessed known rust defenses; six parents from Interior Washington, and Idaho, were considered somewhat resistant to rust, whereas 12 parents from BC (six from the Coastal zone and six from the Interior zone) were untested previously. All seedlings were inspected annually in transplant beds, where rust symptoms and stages were recorded.

A pooled source, composed of aeciospores from six lower-Coastal BC locations, was the most virulent, judged by infection percentage, highest mean spots per seedling, lowest spots-only response, shortest latency, greatest aecial production, and greatest mortality of infected seedlings. Combined data from the two Coastal rust sources, (pooled and Cowichan) demonstrated more virulence than both Interior sources (Nakusp and Valemount). No evidence was found to suggest that a unique race exists in the Cowichan source that overcomes spots-only resistance. Screening Interior western white pine for resistance to blister rust with pooled Coastal rust sources would be superior to using single or pooled Interior rust sources; therefore, only one Coastal inoculation facility is necessary to screen seedlings for both Coastal and Interior zones.

Introduction

The introduction of white pine blister rust (*Cronartium ribicola* J.C. Fisch.) to western North America produced a devastating epidemic in highly susceptible hosts, especially western white pine (*Pinus monticola* D. Don) (Bingham 1983). Within western white pine's range the gene pool of the rust is limited (White et al. 1996), probably because the introduction is known to have occurred only once from one nursery in France (Boyce 1948). This would suggest that differences in infection success would reflect mainly differences in host susceptibility. Exceptions are known, for virulence variation due to the rust has been demonstrated in a few locations (Kinloch and Comstock 1981, Kinloch and Dupper 1987, McDonald et al. 1984). Blister-rust-resistant selections from Idaho are highly susceptible near Cowichan, British Columbia (BC), but not elsewhere in BC, possibly because the gene pool of the rust is unique in this area (Hunt and Meagher 1989).

Such reports, and experience in plantations in BC (Hunt and Meagher 1989; Meagher 1988) indicated that rust screening for a white pine improvement program in BC (Meagher et al. 1990) might require use of different rust sources, perhaps different sources for each of two seed zones (Meagher and Hunt 1999). A trial to test for differences among rust sources in ability to infect seedlings and develop later stages, using aeciospores from four rust sources from BC, was initiated in 1987. Analyses of rust-spot (foliar lesion by rust) number per seedling and spot color at the first inspection were reported by Meagher (1991). Data of further infection success, rust development and seedling survival are analyzed here, to determine if separate rust sources and screening facilities are recommended for these two zones.

Material and Methods

Aeciospores from two Interior sources, Nakusp and Valemount, and two Coastal sources, Cowichan and " pooled" (Figure 1), were inoculated onto isolated wild groves of *Ribes bracteosum* Dougl. or cultivated *Ribes* spp. in spring, 1987. The pooled source was composed of leaves from groves infected separately by aeciospores from six Coastal rust sources, excluding Cowichan. A pooled Coastal source was chosen because it would be practical to collect aeciospores annually from

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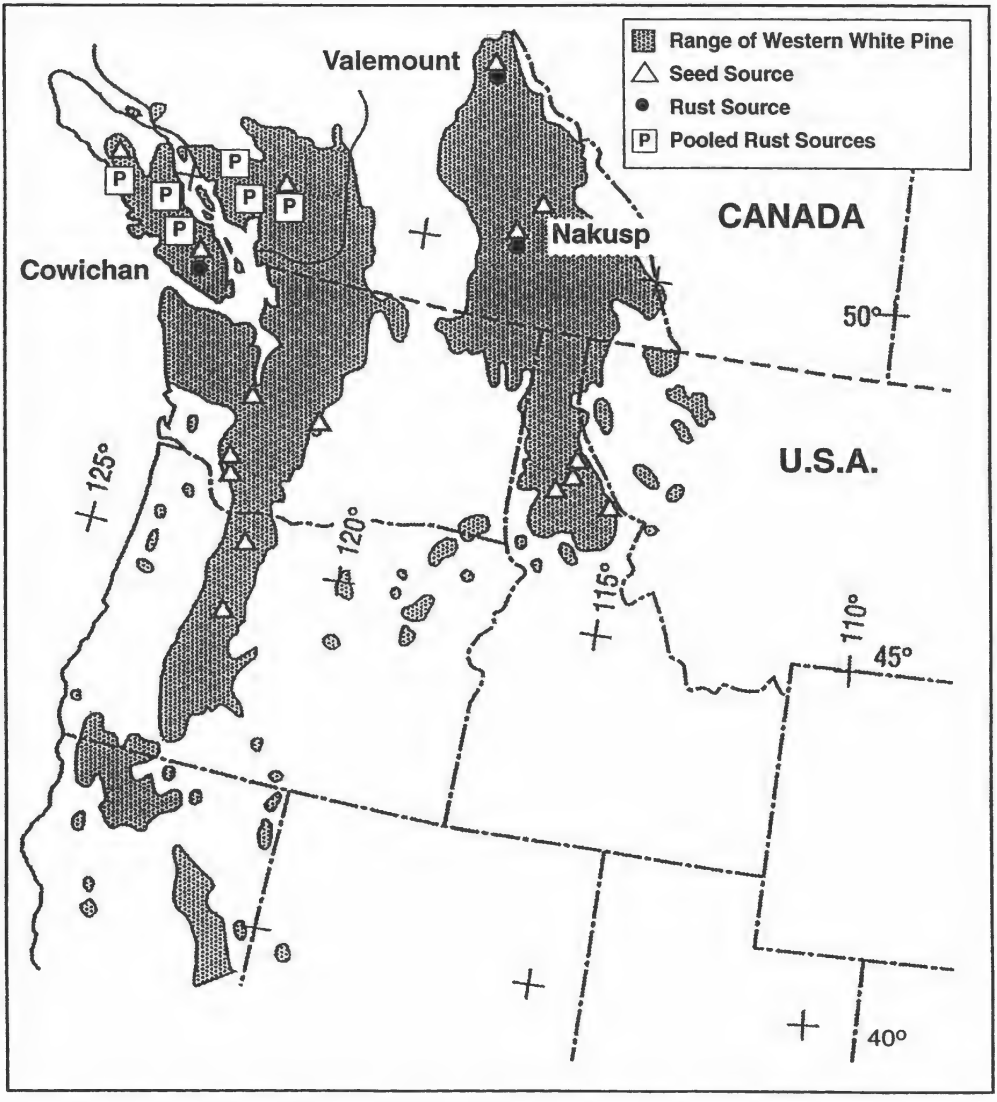

Figure 1. Northern range of *Pinus monticola* (stippled) showing sources of seed and rust sources

several Coastal sources, while it would be very difficult to make such collections from Interior sources, for annual screening trials. At each location (Figure 1) aeciospores were collected from a minimum of six blister rust cankers. Inoculation (Hunt 1988) of 2–year old seedlings occurred in a Coastal facility in September. Seed parents were located in each of two seed zones, Coastal and Interior, with six parents chosen from each of four regions [BC Coast, United States (US) Coast, BC Interior, and US Interior]. Parents from BC had not been tested vs. blister rust, whereas US parents had been tested, and selected. Each parent was represented by up to 10 seedlings in a row of movable Ray Leach "fir" cells® (Canby OR) per replicate. Sets, representing each par-

ent, were randomized in 10 replicates per rust source.

Following spot counting, and classifying spots by color the next spring, all seedlings were transplanted in prepared ground near Victoria, BC. Seedlings were planted in replicate plots per seedlot within rust source with seedling identity in each replicate maintained to permit full concordance with earlier data per seedling. Seedlot and plot (replicate) number were marked on a stake at the start of each plot.

Inspection of each seedling was conducted annually, beginning in spring, 1989, and continuing to1993. In general, we followed the protocol of Hoff and McDonald (1980) with progressive rust stages recorded per seedling, as follows:

0 No rust signs or symptoms

1 Stem orange colored (sign), or rust spots (symptom) on 2-year leaves

2 Needle bases gouty (symptom)

3 Stem swollen (symptom) and orange colored (sign)

4 Pycnia produced (sign)

5 Aecia produced (sign)

6 Slow-canker-growth resistance (see Hunt 1997). This trait was recorded through to 1995.

Due to a change in property management, an entire bed of stock, including all of three seedlots, and part of another seedlot in the Nakusp rust source and most of one seedlot in the Valemount rust source, was removed after the 1990 inspection. Furthermore, inadequate soil drainage reduced survival sporadically throughout the transplant beds. Seedlings in such areas were omitted from the calculation of survival among seedlots and rusts.

Data analyses

Following examination of residuals, ARCSIN transformation of proportion data was used to attain normality.

Analyses of variance were conducted using SAS for Student-Neuman-Keuls (SNK) multiple-range testing at $P \leq 0.05$. Parameters tested were:

1. Infection success: proportion of seedlings infected with rust (showing any sign or symptom of rust, including spotted leaves in 1988).
2. Spots only (including needle shed): proportion of seedlings that shed spotted leaves, by spring 1989, or which exhibited no further rust symptoms, though spotted in 1988 [see McDonald and Hoff (1970) and Bingham (1983) for a description of this resistance].
3. Latency: mean years to first signs of stem rust (orange discoloration in the bark), by inspection year.
4. Aecial stage: proportion of infected seedlings exhibiting aecial stage, by year.
5. Slow-canker growth: proportion of infected seedlings exhibiting slow-canker growth.
6. Mortality: proportion of infected seedlings dead to date, by year.

All effects but replicate in rust were considered fixed. "Error" mean square was the testing term for all effects in the analytical model:

$$\text{Effect} = \text{mean} + \sigma^2_{\text{Rust source}} + \sigma^2_{\text{Rep (Rust source)}} + \sigma^2_{\text{Country}} + \sigma^2_{\text{Rust source (Zone)}} + \sigma^2_{\text{Region}} + \sigma^2_{\text{Parent (Region)}} + \sigma^2_{\text{Rust source*Region}} + \sigma^2_{\text{Parent(Region) * Rust source}} + \sigma^2_{\text{Error}}$$

Least-squares regression correlations of the later stages of development with rust spots were conducted on family mean spots per seedling, averaged among replicates within rust source. When results were combined across rusts, intra-rust spot means by family still were used, resulting in increased degrees of freedom.

Results

Infection success

Infection, here and elsewhere in the manuscript, is defined as seedlings with spots or other advanced symptoms or signs of rust. Results from 1990, 33 months after inoculation, are discussed here (Table 1a) because they are based on material prior to the removal of any stock and losses due to inadequate soil drainage. Infection by rust source varied from 59% (pooled) to 30% (Cowichan). However, Coastal rust sources, pooled and Cowichan, produced similar infection rates (44%) to both Interior rust sources, Nakusp and Valemount, (38%).

Infection differed by country (33% for US vs. 49% for Canada) ($P<0.0001$), by country in seed

TABLE 1a. Rust-infection percentage[1] of inoculated *Pinus monticola* in 1990, by seed source and rust source.

Seed Source		Rust Source[2]						
		Coastal			Interior			Mean
Country	Region	Pooled	Cow	Zonal mean	Nak	Vale	Zonal mean	all sources
Canada	BC Coast	69.5	32.2	50.8	32.4	49.8	41.1	46.0
	BC Interior	74.9	36.7	55.8	41.5	57.1	49.3	52.5
	Mean	72.3	34.4	53.3	36.9	53.5	45.2	49.2 A[3]
U.S.A.	US Coast	49.9	26.3	38.1	33.6	29.3	31.5	34.7
	US Interior	39.9	23.2	31.6	29.3	35.2	32.2	31.9
	Mean	44.9	24.8	34.8	31.5	32.2	31.8	33.3 B
	Mean all	58.5	29.6	44.1	34.2	42.8	38.5	41.3
		A	C		BC	B		
				A			A	

[1] Mean of percentage of infected seedlings by seed parent.
[2] Source of aeciospores. Pooled = a mix of Coastal sources; Cow = Cowichan; Nak = Nakusp; Vale = Valemount.
[3] Corresponding means followed by the same letter do not differ at $P \leq 0.05$ per the Student-Neuman-Keuls (SNK) test.

TABLE 1b. Analysis of variance of rust-infection percentage in 1990.

Source	df	Mean Square	F	Prob.
Rust source	3	3.616	88.1	0.0001
Rep (Rust source)	36	0.157	3.8	0.0001
Seed country ["Country"]	1	6.348	154.6	0.0001
Seed zone	1	0.587	14.3	0.0002
Country X Zone ["Region"]	1	0.859	20.9	0.0001
Parent (Region)	20	0.406	9.9	0.0001
Rust source X Country	3	0.342	8.3	0.0001
Rust source X Zone	3	0.041	1.01	0.3872
Rust source X Region	3	0.033	0.80	0.4914
Rust X Parent (Region)	60	0.124	3.02	0.0001
Error	798	0.041		

zone (35% vs. 46%, US vs. Canada, respectively, for Coastal zone and 32% vs. 53% for Interior zone) ($P<0.0001$) (Table 1), and by seed parent in country ($P<0.049$). The most susceptible stock came from the BC Interior region (52.5%), followed by the BC Coast (Table 1a). BC Interior stock consistently showed the highest infection by all rust sources, whereas either US Interior or US Coastal stock exhibited the lowest infection, depending on the rust source. The rust source X country term ($P<0.0001$) reflects mainly the higher susceptibility of seedlings from unscreened Canadian trees, especially to the pooled rust source.

However, the rust source X parent in region ($P<0.0001$) term indicates that the pattern of results is complex. Infection among seedlots ranged between 89.9%, by the pooled source, and 8.0% (US Coastal Seedlot 2444 by the Cowichan source). Positive correlations were found between family mean of rust spots per seedling and percentage of seedlings exhibiting stem signs or symptoms for the Valemount source ($R^2=0.22$, $P<0.012$) for Coastal rusts ($R^2=0.22$, $P<0.0004$) and for all rusts combined ($R^2=0.12$, $P<0.0004$).

Unspotted seedlings

Rust signs developed in 463 of 1424 (32.5%) unspotted seedlings by 1993. The percentage of such seedlings exhibiting rust differed among rust sources (Table 2), being highest from the pooled source and lowest from the Nakusp source. Coastal sources, both pooled and Cowichan, produced a

TABLE 2. Rust-infection percentage[1] to 1993 of unspotted *Pinus monticola* seedlings by seed source and rust source.

Seed Source		Rust Source[2]						
		Coastal			Interior			Mean
Country	Region	Pooled	Cow	Zonal mean	Nak	Vale	Zonal mean	all sources
Canada	BC Coast	61.4	19.9	40.6	12.6	36.7	24.6	32.6
	BC Interior	49.5	47.1	48.3	24.8	48.8	36.8	42.6
	Mean	55.4	33.5	44.4	18.7	42.7	30.7	37.5 A
U.S.A.	US Coast	44.0	32.4	38.2	23.8	39.4	31.6	34.9
	US Interior	40.7	32.8	36.7	11.5	33.7	22.6	29.6
	Mean	42.3	32.6	37.4	17.6	36.5	27.1	32.2 A
	Mean all	48.9	33.0	40.9	18.1	39.6	28.9	34.8
		A[3]	B		C	AB		
				A			B	

[1] Mean of percentage of infected seedlings by seed parent.

[2] Source of aeciospores. Pooled = a mix of Coastal sources; Cow = Cowichan; Nak = Nakusp; Vale = Valemount.

[3] Corresponding means followed by the same letter do not differ at $P \leq 0.05$ per the Student-Neuman-Keuls (SNK) test.

higher infection level than did both Interior sources (Nakusp and Valemount) (Table 2).

Spot Color

Only 1069 seedlings were found displaying one spot. This low frequency and scatter among sources precluded statistical analyses. However, when combined across sources, and grouped by color, "orange" spots were most efficacious (41.3% of 46 seedlings infected), followed by "Reddish" spots (red, red-brown and red-green combined, 61 seedlings) and "Yellowish" spots (yellow, yellow-brown and yellow-green combined, 792 seedlings) both at 36.9%, then by "Brownish" spots (brown and brown-green combined, 170 seedlings) at 26.5%. No obvious pattern between spot color and rust source was apparent.

Spots only

This rust symptom differed by rust source ($P<0.0001$), but also by country of seed origin ($P<0.0001$) and seed parent ($P<0.0001$). The interaction terms rust source X seed zone ($P<0.0177$), rust source X seed region ($P<0.0327$) and rust source X parent in region ($P<0.0005$) also were significant. The highest spots-only (SO) incidence was produced by the Nakusp source (51.3%), whereas the lowest was produced by the pooled source (30.7%) (Table 3).

Canadian seed parents averaged 30.8% showing SO, while US seed parents averaged 50.3%. The rust source X seed zone interaction seems due to the increased incidence of SO by Coastal families vs. Interior rust sources. Family mean rust spots per seedling was correlated negatively with increasing SO for the Valemount source ($R^2=0.60$, $P<0.0011$), for both Coastal ($R^2=0.40$, $P=0.0060$) and Interior sources ($R^2=0.37$, $P<0.0067$) and for all sources combined ($R^2=0.40$, $P<0.0001$).

Latency

Latency was affected by rust source ($P<0.0001$), country of seed origin ($P<0.0001$) and seed parent ($P<0.0001$), but also by the interaction of rust source X seed zone and interaction of rust source X seed parent in zone ($P<0.001$) (Table 4). The pooled source progressed to stem symptoms the quickest (mean time 1.4 years), while the Nakusp source was the slowest (mean time 2.0 years). Canadian seed sources exhibited stem rust significantly earlier than US seed sources: 1.6 vs. 1.9 years. The shortest mean time to exhibit stem rust (0.9 years) was found in a BC Coastal family inoculated with the Cowichan source, whereas the slowest-developing rust (3.1 years) was found in a US Coastal family inoculated with the same source. The rust source X seed zone interaction seems due to the slow development of the Valemount source vs. the pooled source in US

TABLE 3. Percentage[1] of rust-spotted *Pinus monticola* seedlings displaying Spots Only response, by seed source and rust source.

Seed Source		Rust Source[2]						
		Coastal			Interior			Mean
Country	Region	Pooled	Cow	Zonal mean	Nak	Vale	Zonal mean	all sources
Canada	BC Coast	24.5	31.1	27.1	50.2	32.7	41.4	34.9
	BC Interior	18.8	34.0	23.9	31.8	25.4	27.9	26.0
	Mean	21.6	32.3	25.6	42.8	29.0	35.3	30.8 B[3]
U.S.A.	US Coast	40.5	50.4	46.5	55.3	52.8	54.1	49.8
	US Interior	42.9	58.4	51.5	61.3	39.5	50.4	50.9
	Mean	41.5	54.4	48.0	58.3	46.2	52.3	50.3 A
	Mean all	30.7	45.6	37.4	51.3	37.6	44.1	41.0
		C	AB		A	BC		
				A			A	

[1] Mean of seed parents.
[2] Source of aeciospores. Pooled = a mix of Coastal sources; Cow = Cowichan; Nak = Nakusp; Vale = Valemount.
[3] Corresponding means followed by the same letter do not differ at $P \leq 0.05$ per the SNK test.

TABLE 4. Years to first stem symptom of rust (latency) on rust-spotted *Pinus monticola* seedlings[1], by seed source and rust source.

Seed Source		Rust Source[2]						
		Coastal			Interior			Mean
Country	Region	Pooled	Cow	Zonal mean	Nak	Vale	Zonal mean	all sources
Canada	BC Coast	1.38	1.66	1.49	1.79	1.39	1.59	1.55
	BC Interior	1.24	1.62	1.37	1.89	1.61	1.72	1.55
	Mean	1.31	1.64	1.43	1.83	1.50	1.65	1.55 B[3]
U.S.A.	US Coast	1.58	2.18	1.88	1.99	1.62	1.80	1.84
	US Interior	1.40	1.94	1.70	2.43	2.02	2.23	2.00
	Mean	1.51	2.07	1.81	2.21	1.82	2.02	1.92 A
	Mean all	1.40	1.90	1.63	2.04	1.66	1.84	1.71
		C	AB		A	BC		
				B			A	

[1] Mean of seed parents.
[2] Source of aeciospores. Pooled = a mix of Coastal sources; Cow = Cowichan; Nak = Nakusp; Vale = Valemount.
[3] Corresponding means followed by the same letter do not differ at $P \leq 0.05$ per the SNK test.

Interior stock. A positive correlation between latency and reduced family mean rust spots per seedling was found for only both Coastal sources combined (R^2=0.12, P<0.018) and for all sources combined (R^2=0.10, P<0.0015).

Aecial stage

The percentage of infected seedlings developing aecia increased throughout the study. This stage was affected by rust source (P<0.0001) for all years but 1991 (P<0.02) and 1992 (P<0.47). Incidence among sources in 1993 ranged from 57.5% to 39.2% (Table 5), when seedlings inoculated by the pooled source produced significantly (P<0.0001) more aecia than did seedlings inoculated by all other sources. (Table 5). Country of seed origin was always statistically significant for each inspection (P<0.0001 to 0.0235), and seed parent was significant in all years but 1990. Rust source X country of seed parent was statistically

TABLE 5. Percentage[1] of rust-infected *Pinus monticola* seedlings that developed aecia to 1993, by seed source and rust source.

Seed Source		Rust Source[2]						
		Coastal			Interior			Mean
Country	Region	Pooled	Cow	Zonal mean	Nak	Vale	Zonal mean	all sources
Canada	BC Coast	68.7	44.6	59.0	43.9	54.1	49.0	53.6
	BC Interior	62.7	57.9	61.1	32.3	45.2	40.1	50.0
	Mean	65.7	50.3	60.0 A[3]	39.3	49.6	44.9 B	51.9 A
U.S.A.	US Coast	49.4	30.4	39.9	46.4	38.4	42.0	40.9
	US Interior	45.1	36.9	41.0	32.9	34.4	33.6	36.6
	Mean	47.7	33.0	40.4 B	39.0	36.4	37.6 B	38.9 B
	Mean all	57.5 A	40.1 B	49.9 A	39.2 B	43.0 B	41.2 B	45.2

[1] Mean of seed parents.
[2] Source of aeciospores. Pooled = a mix of Coastal sources; Cow = Cowichan; Nak = Nakusp; Vale = Valemount.
[3] Corresponding means followed by the same letter do not differ at $P \leq 0.05$ per the SNK test.

significant in all years, apparently due to reduced aecial production by the Cowichan and Valemount source on US seedlings. The significant rust source X seed zone term ($P<0.015$) seems due to the high value of the pooled source on Coastal stock vs. the low value of the Nakusp source on Interior stock. A significant, positive, correlation with increasing family mean rust spots was found for all sources combined ($R^2=0.09$, $P<0.0029$) and for both Coastal sources combined ($R^2=0.22$, $P<0.0015$).

Slow-canker growth

The incidence of slow-canker growth resistance (SCG) in infected seedlings was low, ranging from 0.3 to 8.3% (Table 6). The previously selected US seed sources had significantly more SCG individuals than the untested BC sources. The

TABLE 6. Percentage[1] of seedlings demonstrating slow-canker growth to 1995, by seed source and rust source.

Seed Source		Rust Source[2]						
		Coastal			Interior			Mean
Country	Region	Pooled	Cow	Zonal mean	Nak	Vale	Zonal mean	all sources
Canada	BC Coast	2.6	0.6	1.6	2.4	2.3	2.4	2.0
	BC Interior	0.5	0.4	0.5	0.3	0.3	0.3	0.4
	Mean	1.6	0.5	1.0	1.5	1.5	1.5	1.2 A[3]
U.S.A.	US Coast	3.1	1.6	2.4	5.0	2.9	4.0	3.2
	US Interior	3.3	4.7	4.2	8.3	4.8	6.4	5.3
	Mean	3.2	3.2	3.2	6.4	3.9	5.1	4.2 B
	Mean all	2.3 AB	1.9 B	2.1	4.6 A	2.8 AB	3.6	2.8
	A	A						

[1] Mean of seed parents.
[2] Source of aeciospores. Pooled = a mix of Coastal sources; Cow = Cowichan; Nak = Nakusp; Vale = Valemount.
[3] Corresponding means followed by the same letter do not differ at $P \leq 0.05$ per the SNK test.

TABLE 7. Percentage[1] mortality of rust-infected seedlings through 1993, by seed source and rust source.

Seed Source		Rust Source[2]						
		Coastal			Interior			Mean
Country	Region	Pooled	Cow	Zonal mean	Nak	Vale	Zonal mean	all sources
Canada	BC Coast	86.5	84.3	85.6	88.0	79.2	83.6	84.5
	BC Interior	95.7	82.3	91.2	79.0	81.6	80.5	85.6
	Mean	91.1	83.5	88.3	84.4	80.4	82.2	85.0 A[3]
U.S.A.	US Coast	87.9	62.5	75.2	68.2	62.3	65.0	70.3
	US Interior	84.4	75.2	79.3	63.5	58.9	61.2	68.9
	Mean	86.5	68.8	77.0	65.6	60.6	63.0	69.7 B
	Mean all	88.6	74.6	82.4	76.0	70.5	72.4	77.4
		A	B		B	B		
				A			B	

[1] Mean of seed parents.

[2] Source of aeciospores. Pooled = a mix of Coastal sources; Cow = Cowichan; Nak = Nakusp; Vale = Valemount.

[3] Corresponding means followed by the same letter do not differ at $P \leq 0.05$ per the SNK test.

Cowichan rust source appeared to lower the incidence of SCG significantly compared to the Nakusp source; however, this did not hold for US seed lots inoculated by the Cowichan rust source (Table 6). The incidence of slow-canker growth was not correlated with family mean spotting ($P<0.45$).

Mortality of Infected Seedlings

This parameter was affected significantly by rust source ($P<0.0001$), country of seed parent ($P<0.0001$), seed parent ($P<0.0010$), the interaction of rust source X country ($P<0.0074$), and the interaction of seed parent X rust source ($P<0.0019$). Mortality averaged 77.4%, but varied among rusts from 88.6% (pooled) to 70.5% (Valemount) (Table 7). Coastal-zone rusts caused greater mortality (82.4%) than did Interior-zone sources (72.4%). Infected US seedlings survived better (69.7% mortality) than did BC seedlings (85.0% mortality). The rust source X country significance seems due to the high impact of the pooled rust source on US stocks vs. the other sources. Nakusp was the only rust source to produce a significant correlation ($R^2=0.25$, $P<0.0124$) between mean spots and mortality. However, there was a significant correlation of mortality with increasing family mean rust spots for all rusts combined ($R^2=0.13$, $P<0.0007$) and for Coastal ($R^2=0.08$, $P<0.0441$) and Interior ($R^2=0.08$, $P<0.0313$) zone rust sources.

Discussion

Differences among the rust sources were found at each stage of this trial, due mainly to the pooled source. It produced the highest average number of spots per seedling and the most 1-spot trees (Meagher 1991), the lowest incidence of SO seedlings, but the highest level of rust development on "unspotted" seedlings, the shortest latency, the highest percentage of seedlings producing aecia, and the highest mortality of infected seedlings. The other rusts showed less distinction. However, the Cowichan source ranked second to the pooled source in low incidence of SO, latency, and aecia percentage. Both Coastal sources (pooled and Cowichan combined) produced more infection, including of "unspotted" seedlings, less SO response, shorter latency, higher aecia percentage and greater mortality of infected seedlings than did Interior sources. These results parallel the pooled source results fairly strongly. Both Coastal sources had a low incidence of SCG compared to the Interior sources, but the difference was significant for only the Cowichan and Nakusp sources. On no-spot and 1-spot seedlings, the pooled source was most successful at progressing to stem infection. Thus, the greater virulence of the pooled source may reflect more genetic breath than was obtained from the point samples of the remaining sources.

Racial variation in the rust, based on spot color (McDonald and Hoff 1975), was summarized by Hoff (1988). Similar spot colors were found in this study and none were associated with specific rust sources.

Because insects disperse pycniospores from one canker to another (Hunt 1985), thus conveying DNA from one infection to another, the resulting aeciospores from a single canker are genetically heterogeneous. Analysis of ribosomal DNA from 24 BC locations, including all of the sources tested here, revealed much intra-site variation, but no consistent geographic pattern (White et al. 1996). Further studies, employing isoenzymes, random-amplified DNA and restriction enzyme polymorphism markers in the rust, found no geographic pattern of variation (Kinloch et al. 1998). Those data are compatible with the results obtained here with the point sources of the rust.

Comparing results from only untested BC parent trees, SO resistance was more frequent against Interior rust sources, especially Nakusp, than against Coastal sources (Table 3). This trend was apparent in US parent trees (Table 3), which were selected for known infectability and putative resistance mechanisms, including SO (Meagher 1991). Previously, Hunt and Meagher (1985) suggested that a new strain may be responsible for failure of plantations possessing needle-shed resistance (a type of SO resistance) at Cowichan. In this study, SO resistance is significantly less with Coastal rust sources compared to Interior sources (Table 3), suggesting that gene-frequency differences may cause greater virulence in Coastal sources, including Cowichan. However, this did not result in increased mortality, since mortality was similar with the Cowichan rust source and the pooled or Interior sources in all stocks (Table 7). Similar mortality with all sources suggests that Coastal environmental factors are more important in reducing the effectiveness of needle-shed resistance than are the rust sources. Plantations of stocks possessing needle-shed resistance exhibit good field resistance in the Interior of BC and on a high-elevation Coastal site (Hunt 1994), perhaps because the growing season for the rust is short compared to on low-elevation Coastal sites.

Latency of our most-virulent source (pooled) was the shortest; in contrast, McDonald et al. (1984) found that the more-virulent Champion Mine source displayed increased latency, as well as reduced needle shed.

Analyses of variance show that rust source always was a factor in a significant interaction term, and that seed parent generally was included in the same interaction, indicating that the parents responded differently to the sources employed. Therefore, variation in host response to blister rust can be attributed to variability in the host or pathogen, or both. Similarly complex interaction was found in analyses of rust-spot frequency in this same test (Meagher 1991), so persistence of this interaction is not unexpected.

Correlations with increasing mean spots per parent were found for factors associated with increased infection, i.e., stem signs and symptoms, and greater mortality, while correlations with fewer mean spots per parent were found with increasing latency and increasing SO. Perhaps selecting families for reduced spotting is not only a selection for less infection, but also for these other resistant traits. This needs further investigation. SCG seems to be independent of needle spotting frequency.

All families screened in our programs for selection of seed-orchard material in BC have been subjected to inoculation by a pooled mixture of Coastal rust sources at one Coastal facility. The use of a pooled mixture satisfies logistics when obtaining aeciospores for *Ribes* inoculations and results in a stern test of our selected materials.

Acknowledgements

The assistance of the following is acknowledged with gratitude: Dr. P. Theisen, Portland, OR, Dr. R.J. Steinhoff, Dorena, OR and G.C. Franc, Moscow, ID, all of the US. Forest Service, for supplying seeds from US. parents; Silviculture Branch, BC. Forest Service, for supplying inoculation and transplant facilities and funding for seedling inspections and maintenance; H. Craig, D. Craigdallie, J. Dronzek, G. Jensen and G. Lait, Canadian Forest Service, for technical support. The diligence and helpful suggestions of E. Allen, G. Jensen and E. White of the Pacific Forestry Centre are gratefully acknowledged.

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Received 2 February 1999
Accepted for Publication 29 June 1999

Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect) to the Editor.

John H. Michael, Jr., Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, Washington 98501-1091

The Future of Washington Salmon: Extinction Is Not an Option but May Be the Preferred Alternative

Introduction

Puget Sound and much of the northern half of Washington on both sides of the Cascade Range had essentially no anadromous fish 15,000 years ago because the entire area was glaciated. When humans first arrived in the Pacific Northwest, following glacial retreat, salmon were abundant. The fish runs were in dynamic equilibrium with their habitat. They went through periods of abundance, scarcity, local extinction, and re-invasion. Now, due to the impact of humans and the changes they have brought to the area, these populations are threatened with extinction.

The recent and potential future listings of Pacific Northwest salmonids under the United States Endangered Species Act (ESA) have required regional planners, politicians, and the public to examine ways to continue to encourage and maintain development while advocating restoring wild salmonid populations to harvestable levels. In Washington, the response in the press from leaders and the public at large is that extinction of wild salmonids is not an option; the state will take whatever actions are necessary to preserve and restore wild salmonid populations. In this paper, I present a distillation of discussions with fellow biologists—people directly involved with the daily management of salmonid runs, habitat protection and restoration, and recovery programs for specific populations.

In these discussions, I found widespread consensus that society has made a series of essentially irreversible land- and resource-use decisions which have altered the landscape to such an extent that some streams and watersheds can no longer produce anadromous salmonid populations large enough to support harvest if they are able to maintain a self-sustaining wild population at all. There is little likelihood that society will accept, support, or pay for the removal of the infrastructure and industries which have been so damaging to salmonid habitat. Because of these landscape changes, resource managers should concentrate habitat restoration efforts on those watersheds with the highest probability of maintaining anadromous salmonid production and productive habitat. Society should retain anadromous salmonid habitat wherever it exists, and develop fish culture and selective harvest techniques which will provide the levels of harvest demanded by society. The aquatic habitats we preserve or restore will differ significantly from the habitats that were there in the past. The fish populations

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will, likewise, be different, but, if allowed to naturally reproduce, the fish populations will adapt to the existing environment. Given the choices already made by our society, our goal should be to restore naturally spawning salmonid populations wherever possible, then accept that the fish will either evolve to be genetically, physiologically, and behaviorally fit enough to survive in the environment in which it finds itself, or it will go extinct. Reestablishing anadromous salmonids means providing suitable habitat for all life stages and in all areas used by salmonids. For example, a pristine headwater spawning stream is useless to anadromous fish if the lower reaches of the watershed are so deficient in oxygen that adults can not pass through on their upstream migrations or if there are man-made barriers which prevent migration.

Habitat Issues

Water is the most critical component of the salmonid environment. If the water is not the proper temperature, or does not have the proper chemical makeup, the fish can not survive. Water is just as critical to humans. The current human population of Washington needs water for domestic use, for irrigation, for manufacturing, and for the generation of electricity. As the human population grows, it will demand more water. Surface water removal directly diminishes the amount of water available to support and produce fish. As flows decrease, the stream habitat changes, resulting in different relative abundances of the various salmonid species because each species occupies a different niche within a stream. At low enough flows, some species will be eliminated.

In Washington, the solution most commonly offered to the water quantity problem is to set a minimum flow for a stream and then prohibit withdrawals when that minimum is reached. This minimum flow is normally established to meet some critical aspect of a fish's life history such as rearing during the summer, spawning in the fall, or migration in the spring. While setting a minimum flow does set a floor value it also sets a target for users to hit. Any water in excess of the identified minimum is seen as available for out-of-channel uses. The real purpose of setting a minimum flow is to define the level of water-supported growth and industry which will be allowed in a watershed. A possible compromise that would benefit aquatic organisms would be to require that all diversions where water is not consumed through evaporation, evapotranspiration, uptake by plants, animals or humans, or inclusion in a manufacturing process, must be returned to the point of diversion with the same quality as when it was removed. Why is so much freshwater used once and discharged in marine waters and why is wastewater not returned to the point of diversion?

A second problem associated with water is not too little but too much. Floods have a profound effect on in-stream habitat. Periodic over-the-bank flooding, under a natural hydrologic regime, is necessary to maintain high quality in-stream habitat. But under the altered hydrologic regimes brought about by logging and development in a watershed, floods are almost always detrimental to salmonid fish. Impervious surfaces do not allow water to infiltrate the soil. Logged hillsides and associated road systems similarly produce runoff rather than infiltration such that a storm generates more runoff and generates it more quickly than historically.

What do we do with floodwaters? We try to confine them between levees, rock armor the banks, straighten the channels, place streams in underground culverts, and clear out the streams so that the water will pass by quickly. These actions lead to higher velocities which increase movement of streambed gravels which kills eggs. The ability of a stream to move material increases with increases in velocity. As velocity increases both the size of particle moved and the total amount of material moved increases. For example, if the velocity is doubled, the volume of the largest rock fragment that can be transported may be increased by as much as 64 times. If the velocity of the water at the surface of the streambed can be reduced, the redds and their incubating eggs would be protected. If a stream's floodway is widened the velocities can be kept lower, improving egg survival. Setting back levees will substantially reduce stream velocities. There is, however, a downside to widening the stream channel. If water withdrawals lower summer flows, and development increases winter flows, then the resulting stream will have summer flows that are low, warm, and perhaps intermittent, because the channel necessary to carry the flood flows is so much larger than that necessary to carry the summer flow. This increased channel width may place riparian trees well away from the summer watercourse limiting

their ability to provide shade to keep the water cool. The stream then becomes more suited to the production of species which only incubate eggs in the stream (pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*)) rather than those species with extensive summer and winter rearing in the stream (chinook (*O. tsawytscha*), coho (*O. kisutch*), steelhead (*O. mykiss*), cutthroat (*O. clarki*), native char (*Salvelinus malma* and *S. confluentus*)).

In order to return a watershed to a more natural hydrology, it will be necessary to remove levees away from streams in order to increase the flood plain, relocate flood plain houses and businesses, replace road and railroad fills with causeways, and develop methods to slow runoff in developed areas, agricultural areas, and in industrial logging areas so that flooding is proportionate to that which would occur if the ecosystem were intact. Will this be done in Washington?

Any decisions about streamflow issues in Washington will establish a new hydrologic cycle and therefore a new environment to which anadromous salmonids must respond, just as earthquakes, volcanic eruptions, and glaciation challenged them in the past. If enough fish are allowed to spawn, I believe they will successfully adapt in those new environments which meet their overall needs. These fish will be different from those present 200 years ago. No law, no matter how well intended, can alter the biological reality that if the habitat is not suited for a particular species, that organism will not survive. This happens when volcanoes erupt or when new shopping centers, subdivisions, and highways are built. Once the stream reaches some sort of stability, fish may re-invade if there is a population in connected waterways, if migratory paths are not blocked, and if there is sufficient high quality water.

A critical component of salmonid habitat is the estuary. Estuaries provide a gradient between fresh and salt water that helps fish make the physiological adjustment between the two, and they are food rich areas where juvenile salmonids grow rapidly before moving to the high seas. Washington's estuaries are quite different than they were in 1750. They have been filled, tidelands have been turned into uplands, shallow areas have been dredged, and freshwater input patterns have been changed. The resulting estuary will support entirely different animal and plant communities because the habitat is different. Are we going to restore the highly industrialized estuaries of the Duwamish, Puyallup, and Snohomish estuaries or the agriculturally developed Stillaguamish, Skagit, and Nooksack estuaries to a more hospitable environment for salmonids?

Harvest

Salmonid harvest management in Washington is complicated because there are more demands for fish than there are fish available. Sport, commercial, and subsistence fishing have played a large part of Washington's history and economy. There is a strong emotional connection to the harvest and consumption of salmonids that often blocks dispassionate management. This passion for harvest means that survival of salmonids is insufficient; salmonid populations must be robust enough to withstand large harvests.

Recent studies of the relationship between anadromous salmonids, the nutrients they carry in their bodies, and the function of terrestrial and aquatic ecosystems in the Pacific Northwest show that salmon and other anadromous fishes at one time provided the nutrients that were used extensively by many plants, birds, animals and other fish in the ecosystem. These studies show that Washington's recent spawning escapements have been anywhere from one half to one tenth (or less) of the number required to meet the needs of the ecosystem. Will fisheries be restricted sufficiently to allow for this level of spawning?

In some cases, fisheries have been restricted and the result has been large spawning escapements. These escapements have been well above the identified escapement goal. These streams should be intensively studied to determine the overall impact of these large escapements on the entire ecosystem. Will we invest sufficient time and money on these questions in order to provide decision makers with scientifically defensible answers?

Hydropower

The hydropower system is the biggest impediment to anadromous salmonid population recovery in the Columbia River watershed. Even if it were possible to engineer dams so that migrating adult and juvenile fish suffered little mortality when passing through the reservoir and dam, construction of the dam and reservoir has destroyed spawning and rearing habitat through inundation. In the

mainstem Columbia and Snake rivers alone, more than 90% of the spawning habitat upstream of Bonneville Dam has been inundated. It can be recovered only by dam removal. Not only are the fish themselves lost, but the nutrients which they transported from the ocean to fuel the ecosystem are also lost. The same can be said for any dam that blocks anadromous fish migration.

Hatchery Management

Hatcheries, their existence, and the manner in which they are used are the centerpiece of debate in Washington. Arguments range from hatcheries being the source of all current salmonid problems to hatcheries being the answer to all problems. A key to understanding the debate is to recognize that the management of hatcheries (how fish are actually cultured) and hatchery management (how the fish are used in fisheries) are two entirely different topics. My primary intent here is to discuss hatchery management. It is unfortunate that we have been unable to appropriately manage the ease with which salmonids can be cultured. We have used this ease of culture to justify inherently poor fisheries and habitat management decisions. Ease of culture of salmonids has allowed society to justify decisions to destroy habitat or overharvest naturally produced fish populations. Habitat destroyed by dam construction is mitigated by building a hatchery. The hatcheries on the Cowlitz, Lewis, and Columbia rivers demonstrate this. Hatcheries also produce fish to create fisheries. It is particularly destructive when brook (*Salmo fontinalis*), brown (*S. trutta*), rainbow, and lake (*S. namaycush*) trouts, and a plethora of Centrarchids, Percids, and Esocids are stocked into waters accessible to native salmonids because the native fish were deemed to be not as desirable as the introductions.

Hatcheries are much more efficient than nature at producing salmonids for harvest. Fewer spawners, less water, and less land base are needed by a hatchery to produce an equivalent number of fish. The Hood Canal Hatchery has produced, catch plus escapement, chum salmon runs in excess of 300,000 fish. This hatchery has a water right for 0.5 m^3/sec of freshwater from Finch Creek. This freshwater is used to produce a run of chum salmon that in the last decade or so has generally been about twice as large as the chum salmon run produced by the entire Skagit River watershed (8,000 km^2). The Hood Canal Hatchery water supply occupies a fraction of the area occupied by the Skagit watershed. From a pure benefit/cost analysis, producing chum salmon at a hatchery as successful as Hood Canal frees up the whole Skagit watershed for the production of wood fiber, hydroelectric generation, agriculture, and whatever other uses society decides are more valuable than wild chum salmon. Another advantage of artificially produced runs is that they are inherently more stable than a naturally produced run. Most of the mortality on naturally produced salmonids occurs in freshwater. A hatchery, by providing technological fixes to problems of flooding, predation, disease, and loss of habitat can produce a relatively stable annual return. In contrast, a wild run subject to the vagaries of nature will vary over a much wider range of abundances. Again, this is demonstrated by comparison of the Hood Canal Hatchery chum salmon run to the Skagit River watershed. In only one year out of four (basically representing a single brood year) the return of chum salmon to the Skagit is greater than the return to the Hood Canal Hatchery.

It is this success that leads to problems. In order to harvest a high percentage of the Hood Canal hatchery chum at their highest economic value, the decision was made to deliberately overfish the naturally spawning chum in Hood Canal. In the 1970s, the Washington Department of Fisheries found that managing for the identified wild escapement goal of chinook salmon in Puget Sound resulted in surplus fish at the hatcheries and wild escapement goals being unmet due to an effort to catch the hatchery fish. The solution was to lower the wild escapement goal in those systems with hatcheries to a level that could be met under the desired fishing regime, and surpluses of fish at the hatcheries were reduced.

There are alternatives. Fish can be harvested in terminal area fisheries after they have separated from other stocks. Fish can be selectively harvested using specially designed gear that allows fishermen to separate and keep hatchery fish and release naturally produced fish. To accomplish this, hatchery produced fish would have to be externally marked for easy identification, and non-selective gears would have to be eliminated. A major problem of using selective gear in commercial fishing operations is that each fish must be handled and examined. Holding fish awaiting examination in an uncrowded environment will increase the cost per fish.

Conclusion

By our actions, society has already decided that anadromous salmonids in the Pacific Northwest will exist in lower numbers and less diversity than historically. The Duwamish River has had the White River and Lake Washington watersheds removed from it, plus the diversion of water to meet Tacoma's domestic needs. The White and North Fork Skokomish rivers have had large bypass reaches created in order to generate electricity. The estuaries of the Duwamish and Puyallup rivers have been extensively industrialized to where there is little of the functional estuary remaining. Almost every stream in the Puget Sound lowlands has been in some way straightened, diked, or leveed so that the floodplain can be put to agricultural, housing, or industrial use. Most of the mainstem Columbia and Snake Rivers has been converted to reservoirs. Realistically, none of this will change. There is too much money invested, and too much in tax revenues and economic power to remove what is now in place. Consider the difficulty being faced by the proposal to remove the two dams on the Elwha River. The electricity is available elsewhere, they provide essentially no flood protection, and their removal offers the opportunity to restore anadromous salmonid production to an essentially protected watershed. If it is so difficult to act in a situation where the benefits to the natural resources are great and the costs to society small, how can we ever consider restoration of the Columbia or any other developed watershed?

Similar decisions have already been made for other species. Will marshes in the Dakotas, Minnesota, and other parts of the Great Plains be restored to allow whooping cranes (*Grus americana*) to nest in their historic range? Will the Sacramento Valley be restored for pronghorn (*Antilocapra americana*), tule elk (*Cervus elaphus nannodes*), and grizzly bear (*Ursus arctos horribilis*)? Will the key deer (*Odocoileus virginianus clavium*) be restored to all of the Florida Keys? Will we restore the great northern and southern herds of bison (*Bison bison*) to the Great Plains? The policy decisions are plain: species will be maintained in areas where sufficient habitat exists, where that habitat can be preserved, and where existing infrastructure is protected.

In taking a realistic look at the ability of Washington's watersheds to produce anadromous salmonids it is apparent that some difficult choices must be made, and those that have been made must be publicly confirmed. The first is to admit there will be certain watersheds and certain species that cannot be maintained at levels that will support harvest, if they can be maintained at all. The provision for harvest is important because in most of Washington, there are Indian Tribes with treaty rights to harvest anadromous salmonids. The second decision is to make a firm commitment to preserve and restore those watersheds which still offer the opportunity to produce fish. These streams will be where wild anadromous salmonid populations will be restored to levels which will support fisheries The rest of the state will need protection, but any substantial harvest will come from cultured fish.

I mentioned the need to provide harvestable fish. The goal of the ESA is to simply restore and maintain a species so that it will not go extinct. The rights of Washington Treaty Indians require more. The Boldt Decision held that Treaty Indians are entitled to catch fish. The loss of fish through the loss of habitat did not diminish this right. Because most of the causes for the decline in harvest by Washington Treaty Indians can be laid to societal decisions such as water diversions, hydro-electric dams, development, reduction in hatchery programs, and management disagreements with Canada and Alaska, it can be argued that Washington and the Federal Government must operate a hatchery system to replace these lost fish in the Treaty Indian harvest.

The resulting scenario is that some areas of Washington will be retained for wild fish production to protect evolutionarily significant units of a particular species. In the developed areas of Puget Sound and the Columbia Basin, we will recognize that the habitat has been so altered that the cost of producing meaningful numbers of wild anadromous salmonids is too high and that wild anadromous salmonids may become essentially extinct. In these areas there will be extensive artificial-production programs designed to provide desired levels of harvest. Further, the artificially produced fish will all be externally marked so that naturally produced fish can be released when appropriate. These programs, because they are in place to meet a treaty right, will need to be assured of funding. The production of additional fish to allow non-Indians the opportunity to harvest anadromous salmonids can remain a discretionary option for the state and federal budgeting and management authorities.

NORTHWEST SCIENCE

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Ceska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

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Monographs or books

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Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. *In* H. Barnes (ed.) Proceedings of the 9th European Marine Biology Symposium, Aberdeen University Press, Aberdeen. Pp. 363-393.

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Danwiddie, P. W. In Press. Dichotomous key to conifer foliage in the Pacific Northwest. Northwest Science.

Technical Bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agricultural Experiment Station Technical Bulletin 60. Washington State University. 210 p.

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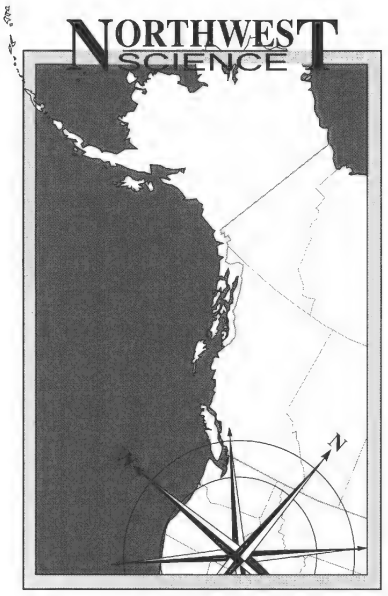

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WSU PRESS Washington State University Press
PO Box 645910
Pullman, Washington 99164-5910 USA

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Northwest Science

Quarterly Publication of the Northwest Scientific Association

Papers published in **Northwest Science** are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts, University Microfilms, Geo Abstracts, GEOBASE,* and *Cambridge Scientific Abstracts, Elsevier BIOBASE/Current Awareness in Biological Sciences.*

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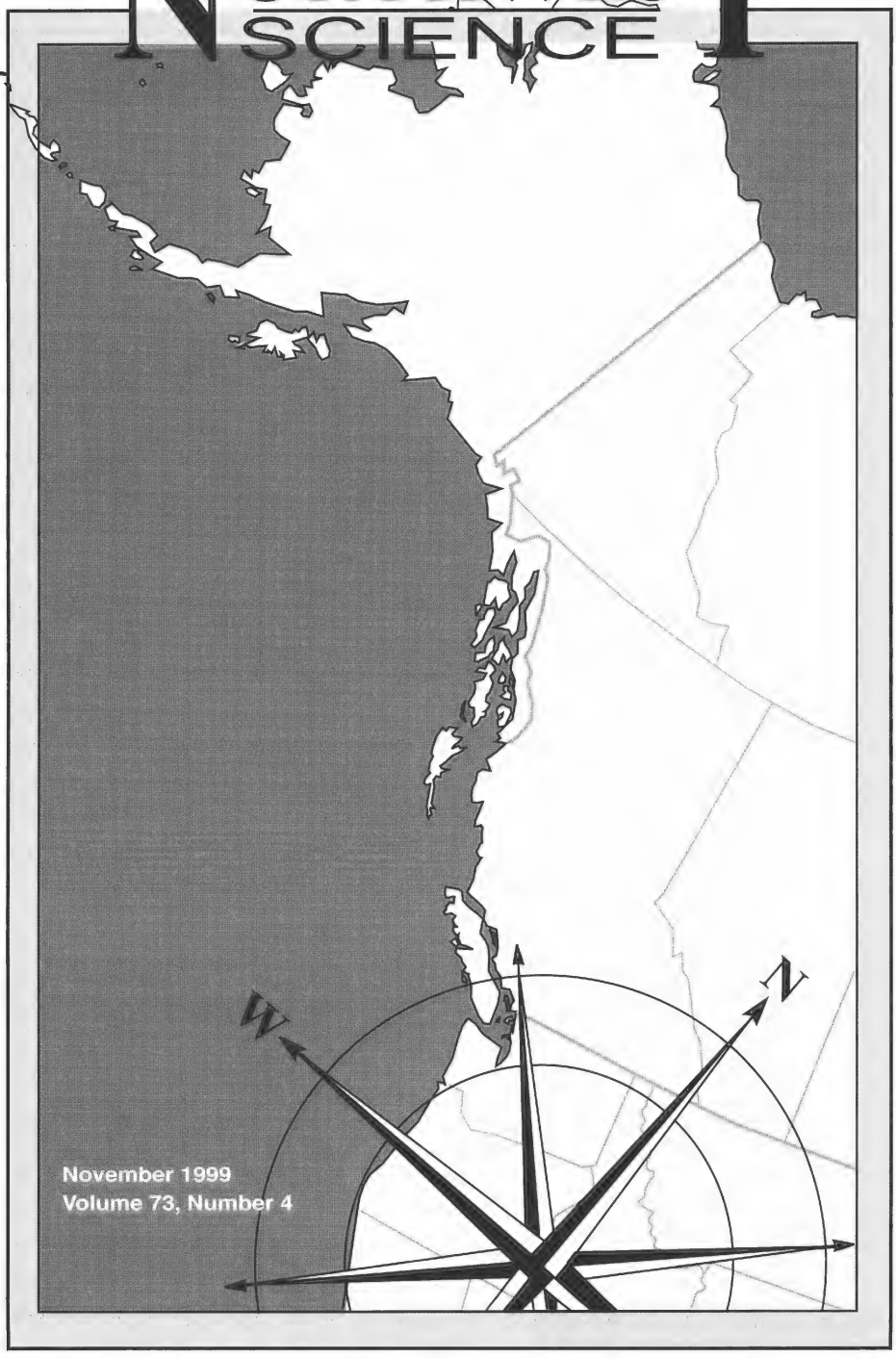

November 1999
Volume 73, Number 4

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals for $25 per year ($10 per year for students). Institutional membership, $40 per year. Sustaining membership, $40 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

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The Northwest Scientific Association is a 501-C(3) tax status organization.

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November 1999 Volume 73, Number 4

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ISSN #0029-344X

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Minutes from the Northwest Scientific Association Business Meeting 26 March 1999, Tacoma, Washington

The 1999 Business Meeting of NWSA was called to order by President Theodore Thomas at 1:15 PM. There were 120 members and officers present. Ted Thomas introduced the members of the Board who were present.

The minutes of the 27 March 1998 Business Meeting were distributed and read by the Secretary, Margaret O'Connell. The minutes were approved.

The Treasurer's report was distributed and read by David Hansen. Dave Hansen reported that income was primarily from dues, with additional monies from CD accounts. He also reported that the 1998 Annual Meetings in Olympia, WA. had generated income. Dave Hansen reported that the major expense of the Society was the WSU Press bill. The treasurer's report was approved.

Ed Schreiner, Editor of *Northwest Science,* had no report.

Ted Thomas announced that the 1999 Outstanding Scientist Award has been awarded to Dr. Douglas Houston. The 1999 Honorary Life Member Award has been awarded to Dr. Robert Edmunds for his long support of the Society. Dr. Edmunds thanked the Society for the award and encouraged all members to submit articles (especially on soils) to Northwest Science.

Ross Black, chair of the Student Awards Committee announced the 4 recipients of the 1999 Student Research Awards: 1) Anthony T. O'Geen, University of Idaho, $1,000, "Evaluation of recharge mechanisms and rates through loess in the Pullman-Moscow Basin using environmental tracers and soil stratigraphy"; 2) Marilyn R. Bartels, Oregon State University, $700, "Conservation of *Sidalcea nelsoniana* (Nelson's checkermallow) through habitat management"; 3) Matthew A. Gitzendanner, Washington State University, $996, "Genetic patterns in the rare plant species *Lomatium cookii* (Apiacea): one species or two?"; 4) David Benson, Washington State University, $942, "The causes and consequences of the evolution of monogamy in white-tailed ptarmigan". R. Black reminded all student members that the deadline for submitting proposals is 15 January and encouraged all to do so.

Richard Cellarius, chair of the Program Committee for the 1998 Annual Meetings announced that income from those meetings would be split proportionately with the Society for Northwestern Vertebrate Biology based on membership attendance.

Ted Thomas introduced Kelly Duffied, program organizer from the University of Washington. Ted Thomas announced that there were 275 attendees at the 1999 meetings, 1/3 of whom were student members. A total of 164 Abstracts were submitted for this year's meeting.

The Nominating Committee presented its nominations for officers and trustees. Two current Board members, Barry Keller, Idaho State University, and Ross Black, Eastern Washington University, were nominated for an additional three-year term. Steve Acker, USDA PNW Research Station, Corvallis, Sarah Green, R. USDA PNW Research Station, Corvallis, and Steve. Rust, Idaho Fish and Game, were nominated for three-year terms. Ted Thomas asked for further nominations from the membership. Hearing none, Jan Henderson moved that the membership elect the candidates and Richard Cellarius seconded the motion. The motion carried.

Ted Thomas expressed his thanks to the board and the membership for their support during the past year. He thanked Kelly Duffield for her help in organizing the meetings. He expressed special appreciation to the National Park Service, Mt. Rainier National Park, and to Gary Ahlstrand of Mt. Rainier National Park for their support and cooperation in hosting the 1999 meetings.

Ted Thomas announced that the 2000 Annual Meetings will be held at the University of Idaho, Moscow, Idaho and invited all to attend. He then called for a motion to adjourn the meeting. Richard Cellarius so moved and Richard Easterly seconded the motion. The 1999 Business Meeting was adjourned at 1:45 PM.

Announcements

Call for Nominations

Please submit your nominations for Outstanding Scientist as well as nominations for officers and trustees. These should be forwarded by 31 December 1999 to the Secretary, David Hansen.

Annual Meeting, University of Idaho, March 16-18, 2000

The 73rd annual meeting of the Northwest Scientific Association will be hosted by the University of Idaho at its campus in Moscow, Idaho, on March 16–18, 2000. Following a business meeting of the governing board on March 16, scientific sessions will occur on the following two days with a variety of concurrent sessions and symposia.

Members and nonmembers are welcome at the meetings, and students are especially encouraged to attend and report the results of their research at the meeting.

A call for abstracts and meeting registration information will be mailed to all members.

David L. Peterson, Darci Bowers, and **Sarah Brace,** U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Cascadia Field Station, Box 352100, Seattle, Washington 98195
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Tropospheric Ozone in the Nisqually River Drainage, Mount Rainier National Park

Abstract

We quantified the summertime distribution of tropospheric ozone in the topographically complex Nisqually River drainage of Mount Rainier National Park from 1994 to 1997. Passive ozone samplers were used along an elevational transect to measure weekly average ozone concentrations ranging from 570 m to 2040 m elevation. Weekly average ozone concentrations were positively correlated with elevation, with the highest concentrations consistently measured at the highest sampling site (Panorama Point). Weekly average ozone concentrations at Mount Rainier National Park are considerably higher than those in the Seattle-Tacoma metropolitan area to the west. The anthropogenic contribution to ozone within the Nisqually drainage was evaluated by comparing measurements at this location with measurements from a "reference" site in the western Olympic Mountains. The comparison suggests there is a significant anthropogenic source of ozone reaching the Cascade Range via atmospheric transport from urban areas to the west. In addition, temporal (week to week) variation in ozone distribution is synchronous within the Nisqually drainage, which indicates that subregional patterns are detectable with weekly averages. The Nisqually drainage is likely the "hot spot" for air pollution in Mount Rainier National Park. By using passive ozone samplers in this drainage in conjunction with a limited number of continuous analyzers, the park will have a robust monitoring approach for measuring tropospheric ozone over time and protecting vegetative and human health.

Introduction

Ozone occurs in the troposphere as a result of photochemical formation from anthropogenic and biogenic precursors (Logan 1985, Finlayson-Pitts and Pitts 1986, Böhm et al. 1991, Finlayson-Pitts and Pitts 1997) and transfer from the stratosphere (Chatfield and Harrison 1977a,b, Viezee et al. 1983, Altshuller and Lefohn 1995, Stockwell et al. 1997). Ozone concentrations are often higher in rural areas than in the pollutant source area, because ozone and ozone precursors are transported downwind while photo-oxidation proceeds during daylight hours (Miller et al. 1986, Pinkerton and Lefohn 1987, Peterson et al. 1991, Lefohn and Manning 1995, Stockwell et al. 1997). Nighttime concentrations in rural areas are often higher as well, because local production of nitric oxide (NO) is minimal, and titration of ozone is low (Logan 1985, Böhm et al. 1991, Böhm 1992, Lefohn 1992).

Western Washington is home to a wide range of ecosystems as well as 4 million people and 3.9 million vehicles (Washington Office of Financial Management 1997). During summertime in the Puget Sound region (where the major cities are located), ozone forms during the daylight hours, with ozone transported eastward toward the Cascade Range foothills and higher elevations (Edmonds and Basabe 1989, Basabe 1992, Cooper and Peterson In Press), resulting in relatively high nighttime concentrations at rural, high-elevation locations (Brace and Peterson 1998). Some of the highest ozone concentrations (> 150 ppbv) have been recorded in Enumclaw (40 km NW of Mount Rainier National Park) at the eastern edge of the Puget Sound regional monitoring network (Washington Department of Ecology 1994). The presence of higher ozone concentrations at the eastern edge of the monitoring network (Steyn et al. 1997) indicates that elevated levels of ambient ozone are degrading the air quality of wildland areas in western Washington (Steenburgh 1995). However, the spatial distribution of ozone has been difficult to infer due to a sparse network of analyzers (Puckett 1995, Haney et al. 1997, Peterson In Press).

The distribution of ozone in rural and mountainous regions has been studied in the Alps (Puxbaum et al. 1990, Wunderli and Gehrig 1990, Loibl et al. 1994, Sandroni et al. 1994), the White Mountains of New Hampshire (Aneja et al. 1994a,b), the Appalachian Mountains (Berry 1964, Zaveri et al. 1995, Skelly et al. 1997), the San Bernardino Mountains in California (Miller et al. 1986, Miller 1992, Bytnerowicz et al. 1999) and the Sierra Nevada (Van Ooy and Carroll 1995,

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Watson et al. 1999). Most studies of ozone in mountainous terrain have used electronic ozone analyzers, which are costly to operate and require a power supply. These limitations make it difficult to establish a monitoring network with sufficient analyzers to accurately quantify spatial variation in ozone exposure at remote locations. However, passive ozone samplers can measure cumulative ozone exposure across a landscape with minimal spatial interpolation of data (Koutrakis et al. 1993, Ray 1996, 1997, Brace and Peterson 1998, Cooper and Peterson In Press).

Tropospheric ozone has become an important air-quality issue in the Puget Sound region, as the human population and number of vehicles continue to increase. National parks and wilderness areas in the Cascade Range east of Puget Sound are afforded Class I air quality protection through the United States Clean Air Act. Better spatial and temporal quantification of tropospheric ozone is needed in Class I areas in order to determine if air quality is being degraded and if human and vegetative health may be at risk. In this study, we used a network of passive ozone samplers to measure summertime ozone exposure in the Nisqually River drainage of Mount Rainier National Park. Measurements were conducted at 5 sites over a 4-year period to characterize spatial variation in tropospheric ozone along an elevational gradient.

Methods

The study was conducted at Mount Rainier National Park 100 km southeast of Seattle in the Cascade Range of Washington state. The Mount Rainier region is dominated by Pacific maritime climate, typified by wintertime westerly low-pressure systems associated with mild temperatures and high precipitation, and by summertime high pressure systems associated with warm temperatures and low precipitation. Warm, dry summertime weather combined with long daylengths that provide an abundance of sunlight create the atmospheric conditions that facilitate ozone synthesis. The highest ozone concentrations occur when an upper level ridge of high pressure builds over the west coast of North America and a thermal trough develops from California northward along the Pacific coast (Barna et al. In Press).

Sampling was conducted during the summers of 1994, 1995, 1996, and 1997. Ozone was sampled at 5 sites along the Nisqually River drainage in Mount Rainier National Park, ranging from an elevation of 570 m (Tahoma Woods, just west of the park boundary) to 2040 m (Panorama Point) (Figure 1). The latter site was sampled in 1995 to 1997 only. Some sites were unavailable during the early summer due to heavy snowpack, and measurements were occasionally missing due to damage to samplers in the field.

Passive ozone samplers (Ogawa & Co.®) were used to measure weekly average ozone concentrations. A sampler consists of a plastic canister containing two nitrite-coated filters. Ozone from the ambient air oxidizes the nitrite into nitrate during the exposure period, and a chemical assay is then conducted for nitrate concentration (Koutrakis et al. 1993). PVC-pipe rainshields protected the filters from direct contact with water and other contaminants. The filter was suspended with its bottom edge flush with the bottom of the rainshield. Filters and rainshields were attached to posts 2 m above the ground.

Passive ozone samplers were installed at sites in clearings at least 20 m from the nearest forest canopy, according to standard sampling protocols (Ray 1997). All sites were located away from roads and obvious sources of air pollutants. One sampler was placed at each site. Duplicate filters were deployed at each site every fourth week to measure precision between samplers. Passive sampler sites were co-located with continuous electronic analyzers (Dasibi Environmental Corp.® model 1008, UV photometric) at Tahoma Woods and at Paradise (1650 m; operated in 1996 and 1997 only) to assess accuracy between samplers and analyzers. The electronic analyzers are maintained with Washington Department of Ecology (1994) quality- assurance protocols (performance specifications include: noise ± 0.001 ppm, flow rate 2 L min^{-1}, precision 0.001 ppm, linearity ± 0.001, stability ± 0.002 ppm at 0.500 ppm, cycle time 10 sec).

Passive sampler filters were exposed for one-week periods. Exposed filters were collected and new filters installed within a few hours on the same day, during a fixed window of time (900 to 1300 hours) so that each sampler's exposure time would be as close to 168 hr (one week) as possible. Passive samplers were placed in sealed plastic bags within vials until deployed by field technicians. Exposure time began when the technician clipped the sampler inside the rainshield, and ended one week later when the technician sealed

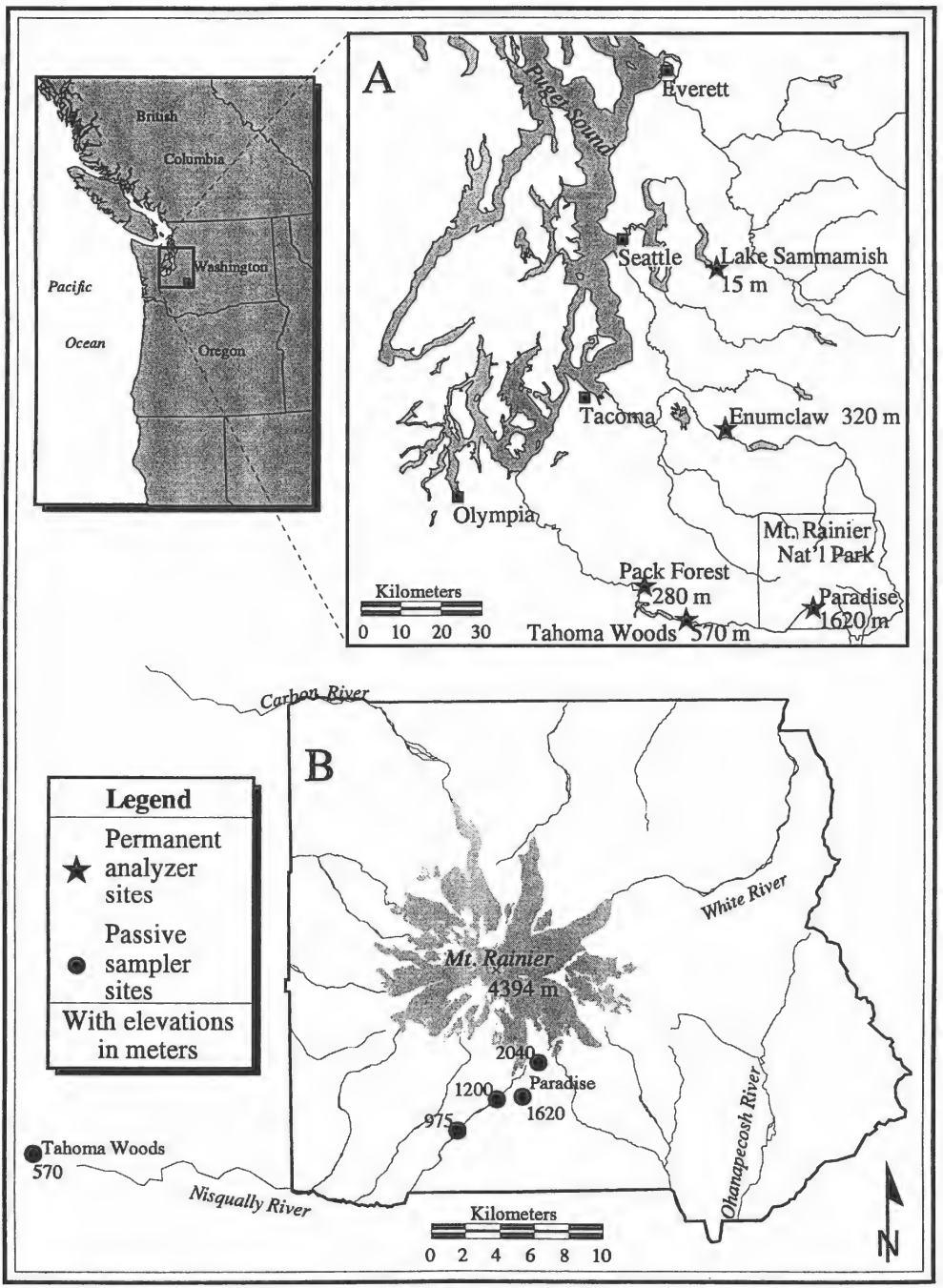

Figure 1. Location of passive ozone samplers and continuous analyzers in the Nisqually River drainage, Mount Rainier National Park.

the sampler in the bag within the vial. Samplers were mailed to Research Triangle Institute (Research Triangle Park, North Carolina, USA) for chemical analysis within 24 hours of removal from the field.

Passive sampler filters were extracted in an ozone-free environment, and ion chromatography was used to quantify nitrate concentration. A fixed volume of 5 ml water was used for the extraction. Weekly average ozone concentration was then calculated as follows (Koutrakis et al. 1993):

$$E_{sample} = [(NO_{3(sample)})*Vol*6.572 \times 10^{3}] * R^{-1}$$
$$E_{blank} = [(NO_{3(blank)})*Vol*6.572 \times 10^{3}] * R^{-1}$$
$$E_{net} = [E_{(sample)} - E_{(blanks)}]$$
$$\{O_3\} = [E_{net} * t^{-1}]$$

where

E = ppbv
$\{O_3\}$ = ozone mixing ratio ($ppbv^{-1}$)
t = exposure time (hr)
R = collection factor (21.6)
Vol = extraction volume (ml)
(NO_3) = nitrate determined by analysis ($\mu g\ ml^{-1}$)

Weekly average ozone concentrations were calculated for each passive-sampler site. Sampler precision was obtained by calculating the percent difference between replicate samplers at each site. Accuracy of measurements between analyzers and samplers was determined by comparing passive sampler values to continuous hourly ozone values for the identical sampling periods. Weekly average ozone concentrations were plotted for each site to detect spatial and temporal variation in ozone concentrations. A seasonal mean was calculated from the weekly average ozone exposures for each site to determine the relationship between weekly average ozone concentration and elevation.

Residual analysis indicated that passive sampler data are normally distributed for all transects. Therefore, simple linear regression was used to develop equations to model the relationship between elevation and ozone concentration for each of the 4 years of data. Analysis of covariance (ANCOVA) was used to test the null hypothesis that the four regression lines were equal, with elevation and year as independent variables, and ozone concentration as the dependent variable; differences between treatments were assessed by testing for differences in slope and intercept.

Results and Discussion

Accuracy and Precision of Passive Ozone Samplers

Weekly average ozone concentration data were compared between passive samplers and continuous analyzers for the Tahoma Woods and Paradise sites with co-located samplers and analyzers. Passive sampler values are slightly higher than analyzer values for Tahoma Woods (mean difference=2.0 ppbv, SD=0.3) and Paradise (mean difference=5.8 ppbv, SD=3.5). Other recent studies found a similar level of accuracy between passive samplers and continuous analyzers (Figueroa et al. 1996, Brace and Peterson 1998, Cooper and Peterson In Press). Differences between passive samplers and analyzers may be partially explained by differences in how the techniques sample ambient air per unit time.

Passive sampler precision was calculated as the percent difference between replicate samplers at each site. The samplers measured ozone with high precision, with a mean percentage difference between replicates of 2.1% (SD=2.4). This value is superior to sampler precision measured in previous analyses in western Washington (Figueroa et al. 1996, Brace and Peterson 1998, Cooper and Peterson In Press).

Spatial Variation in Ozone Exposure

Diurnal Ozone Patterns

Continuous analyzer data for Tahoma Woods indicate that hourly maximum ozone concentration varies greatly over time as a function of temperature (Figure 2). The two-week period of ozone exposure shown here illustrates that ozone synthesis and transport to the Cascade foothills is considerably higher during periods of warmer temperatures (Brace and Peterson 1998), and that diurnal variability is greater on warm days. Summertime temperatures are, of course, higher on days when there is minimal cloud cover, thereby providing more energy to drive ozone synthesis during daylight hours (Seinfeld 1989, Finlayson-Pitts and Pitts 1997).

Continuous analyzer data for Tahoma Woods and Paradise—separated by 30 km horizontal distance and 1050 m elevation—show the difference in diurnal patterns of maximum hourly (i.e., the maximum value during each hour of measurement),

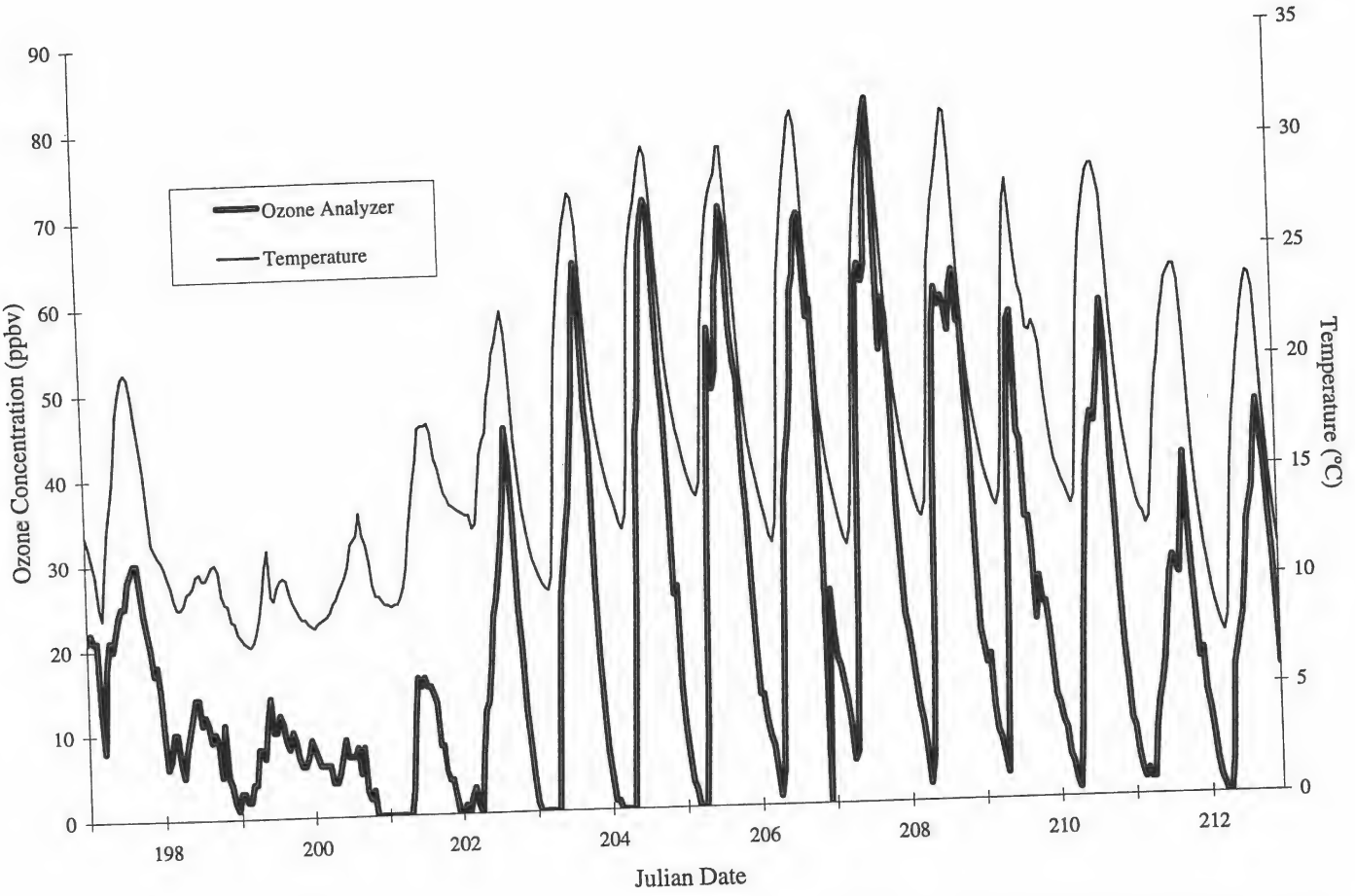

Figure 2. Hourly temperature and hourly maximum (highest analyzer measurement per hour) ozone concentration based on continuous analyzer data for the Tahoma Woods monitoring site, 16 July through 31 July, 1996.

daily maximum, and daily average ozone concentration at these two sites (Figure 3). The sample data shown here (for the same time period as shown in Figure 2) were measured during a period in which cool, cloudy weather was followed by warm, sunny weather. The Paradise site had less diurnal variation in ozone, usually had higher maximum ozone concentration, and always had higher daily average ozone concentration.

The Paradise site had ozone concentrations remaining between 40 and 90 ppbv throughout the day and night during warm weather, compared to 10 to 80 ppbv at Tahoma Woods. Other studies have reported a similar diurnal pattern of ozone exposure at high elevations in Mount Rainier National Park (Brace and Peterson 1998) and other high-elevation sites (Wunderli and Gehrig 1990, Puxbaum et al. 1991, Sandroni et al. 1994, Bytnerowicz et al. 1999, Watson et al. 1999).

Normal atmospheric distribution of ozone grading from the troposphere up to the stratosphere accounts for at least a portion of the higher ozone concentrations at Paradise (Chatfield and Harrison 1977a,b, Viezee et al. 1983, Finlayson-Pitts and Pitts 1986, Altshuller and Lefohn 1995, Stockwell et al. 1997). Ozone is also transported eastward from the greater Seattle-Tacoma metropolitan area by mesoscale circulation activity (Pryor et al. 1995, Steenburgh and Mass In Press), and comprises a proportionally greater component of tropospheric ozone under conditions conducive to synthesis (i.e., warm, sunny weather). It has also been suggested that anabatic winds transport ozone upvalley during the day (Broder and Gygax 1985, Green et al. 1992a,b), and that katabatic winds distribute a portion of ozone from high elevations to valleys at night when these winds are involved in the formation of inversion layers (Fujioka et al. 1999). In the first analytical effort to simulate ozone formation and transport in western Washington, Barna et al. (In Press) combined meteorological modeling (MM5 and Calmet) and photochemical air-quality modeling (Calgrid) to show that ozone does not build up significantly in the Cascades, and that ozone formed on one day is not recirculated within the area through the night but is flushed by relatively clean air on a nearly continuous basis.

Because there are few air pollutant sources at high elevations in the Cascade Mountains, NO concentrations are low, permitting ozone levels to remain elevated throughout the night (Logan 1985, Böhm 1992) and contributing to higher weekly average concentrations. In the valleys (e.g., Tahoma Woods and urban areas to the west) where more NO is available for titration, nighttime ozone concentrations are lower (Loibl et al. 1994). The lack of diurnal variation at higher elevations in the Cascades is typical of "urban transport" or far-from-source sites (Böhm et al. 1991). Lack of diurnal variation may simply be a function of better mixing of ground-level air (and ozone) through the boundary layer in windier conditions at higher elevation, so that local depletion and formation are mixed vertically.

Ozone-Elevation Relationships and Anthropogenic Contribution of Ozone

There was considerable temporal variation in weekly average ozone concentrations within and between sites during each of the 4 summers in which sampling was conducted (Figure 4). Higher-elevation sites in the Nisqually drainage clearly had higher ozone concentrations than lower-elevation sites, although the positive ozone-elevation correlation was not always a perfect one, probably due to variation in air pollutant production and transport as modified by local atmospheric circulation, topography, and vegetation. The highest weekly average for all four years (67 ppbv) was measured at the highest-elevation site. Averages for the entire summer of sampling, an indicator of long-term seasonal exposure, were also highest for the highest-elevation sites. Weekly average ozone concentrations measured at all sites in this study were higher than at lower-elevation sites in the Seattle-Tacoma region to the west (Figueroa et al. 1996, Brace and Peterson 1998). They were also considerably higher than values measured along a "clean" elevation transect in the western Olympic Mountains (Cooper and Peterson In Press) where there are negligible anthropogenic sources of pollution.

Tests for equality of variances among the 4 years of data show no serious departures from homogeneity. The test for equality of regression lines (Figure 5) indicates that the relationship between elevation and ozone could not be sufficiently described by one model ($F_{6,12} = 73.01$, $P < 0.0001$). A test for equal slopes among the regression models further indicates significant differences in the rate of change in ozone concentration with

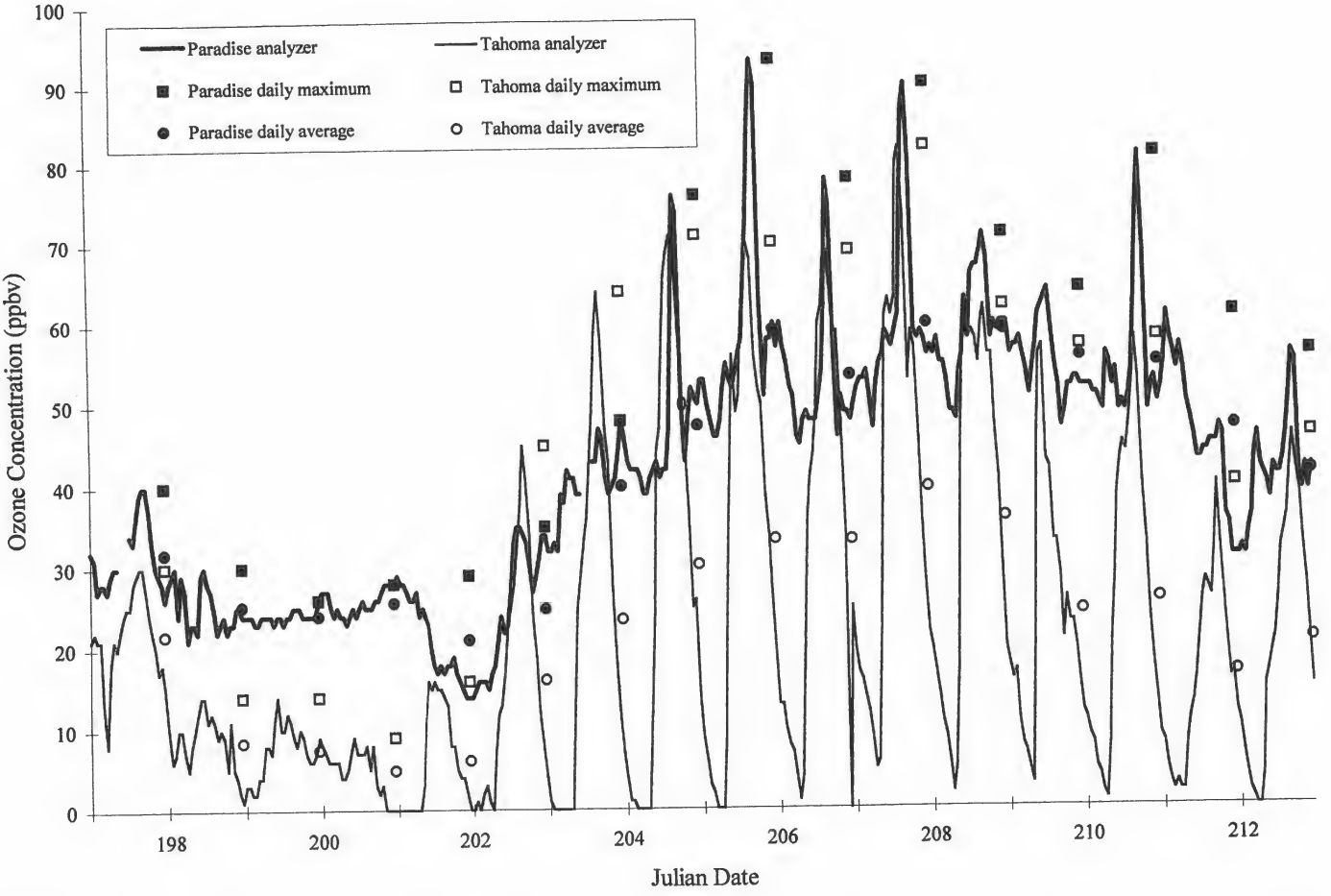

Figure 3. Hourly maximum (highest analyzer measurement per hour), daily maximum, and daily average ozone concentrations based on continuous analyzer data for the Tahoma Woods and Paradise monitoring sites, 16 July through 31 July, 1996.

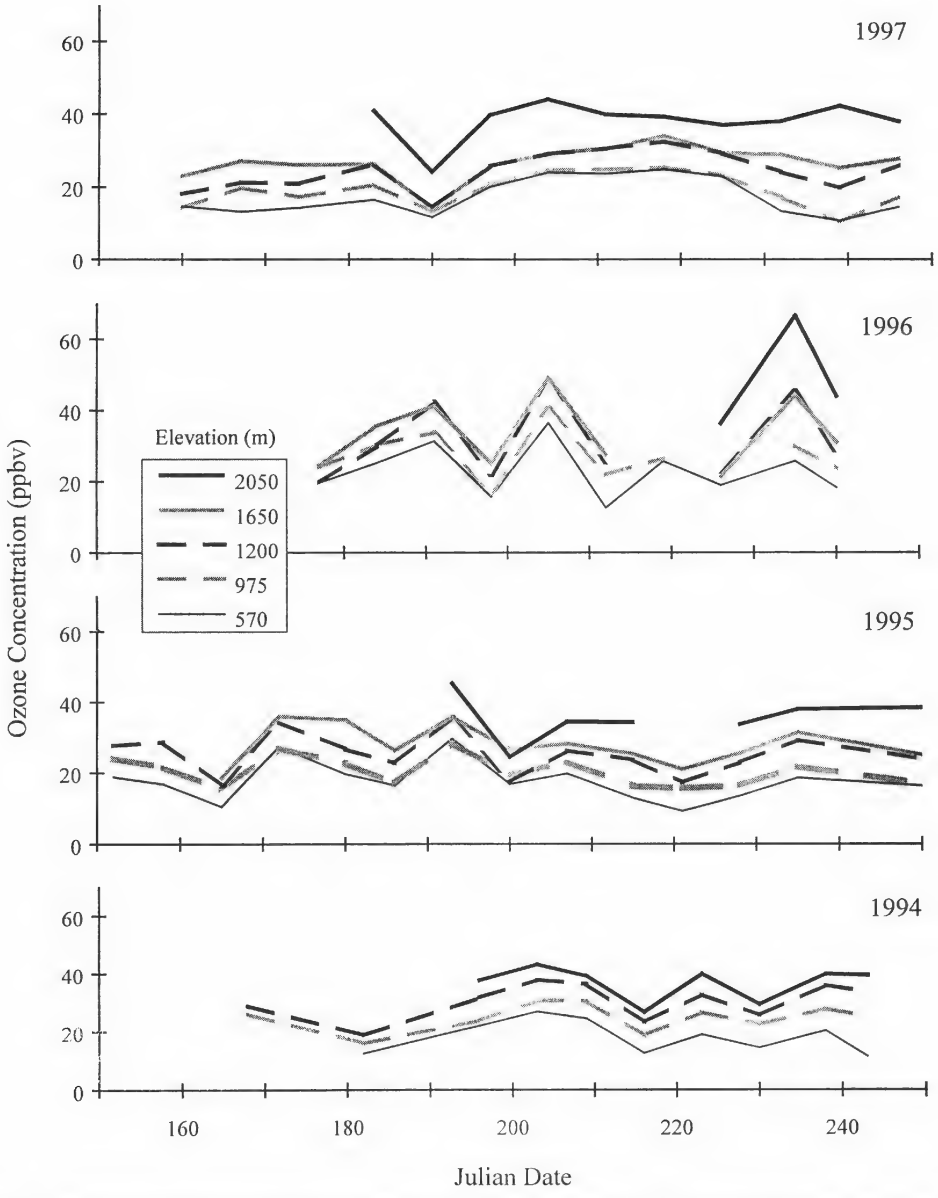

Figure 4. Weekly average ozone concentrations at sites along an elevational gradient in the Nisqually River drainage of Mount Rainier National Park for the summers of 1994 through 1997.

increasing elevation among years ($F_{3,12}$=5.70, P = 0.01). When data for 1994, whose mean squared error is an outlier, is removed from the analysis, the remaining year's slopes are barely statistically equal ($F_{8,2}$ = 4.39, P = 0.052), although further analysis shows that significant differences exist among model intercepts ($F_{10,2}$ = 64.12, P < 0.0001). Pairwise comparisons show equality in slopes for

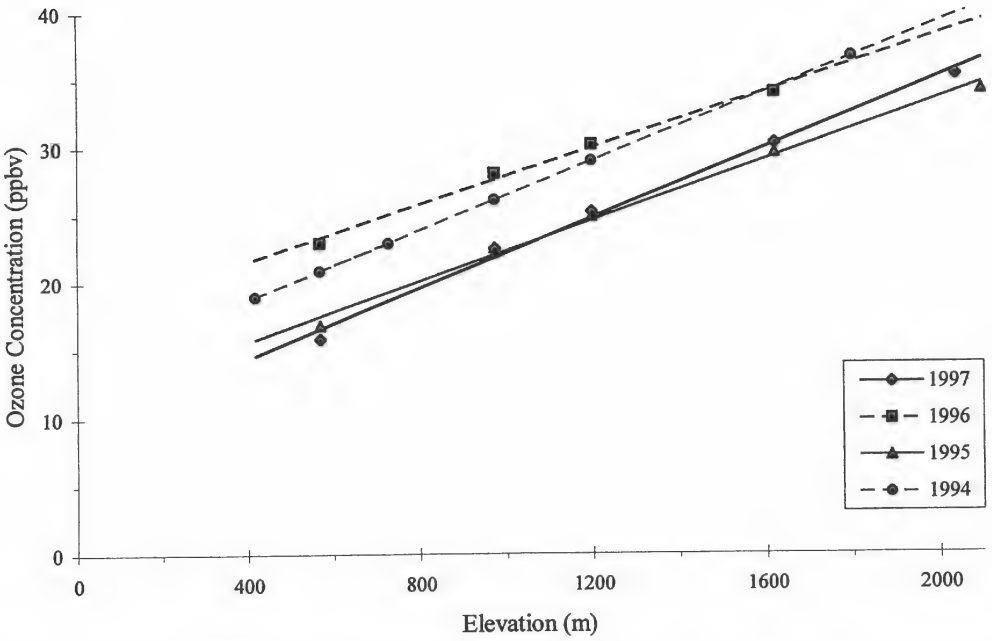

Figure 5. Seasonal averages of passive ozone sampler data for 1994 through 1997. Regression analysis indicates that there is a significant positive correlation (regression coefficient [slope] > 0) between ozone and elevation for each year. Ozone concentration increased a mean of 1.2 ppbv per 100 m elevation gain for the 4 years of summer measurements.

all years ($P > 0.05$) except between 1994 and 1995 ($F_{7,1} = 10.67$, $P = 0.01$), and between 1996 and 1997 ($F_{5,1} = 6.66$, $P = 0.049$). This indicates that the difference between the 1994 and 1995 regression lines is the primary influence in the overall ANCOVA results.

The positive correlation between ozone and elevation is consistent with measurements made on elevation gradients at other locations in the Pacific Northwest (Brace and Peterson 1998, Cooper and Peterson In Press) and other mountainous regions (Wunderli and Gehrig 1990, Puxbaum et al. 1991, Smidt and Herman 1992, Aneja et al. 1994b, Sandroni et al. 1994). Ozone concentration increased a mean of 1.2 ppbv per 100 m elevation gain for the 4 years of summer measurements, which is nearly identical to the ozone-elevation relationship calculated for limited temporal sampling in other drainages in the Mount Rainier region (Brace and Peterson 1998) and other locations in the Cascade and Olympic Mountains (Cooper and Peterson In Press). When distance (rather than elevation) is the independent variable in the regression model, the coefficient is still significantly different from 0, although at a lower P-level; distance is roughly equivalent to elevation with respect to its relationship with weekly average ozone concentration.

The ozone-elevation relationship calculated for the Nisqually drainage indicates that mountain locations on average have higher cumulative exposure to ozone than upwind valley and urban locations. Against a background of higher ozone at higher elevations (Chatfield and Harrison 1977a,b, Viezee et al. 1983, Altshuller and Lefohn 1995), there is a summertime pattern in western Washington of prevailing west-to-northwesterly winds that transport ozone from urban sources to downwind rural locations (Miller et al. 1986, Sandroni et al. 1994, Brace and Peterson 1998, Fujioka et al. 1999). This has been convincingly demonstrated for western Washington through simulation of ozone synthesis and transport, based on emission inventories, analyzer data, and mesoscale meteorological modeling (Barna et al. In Press). This modeling effort indicates that a significant

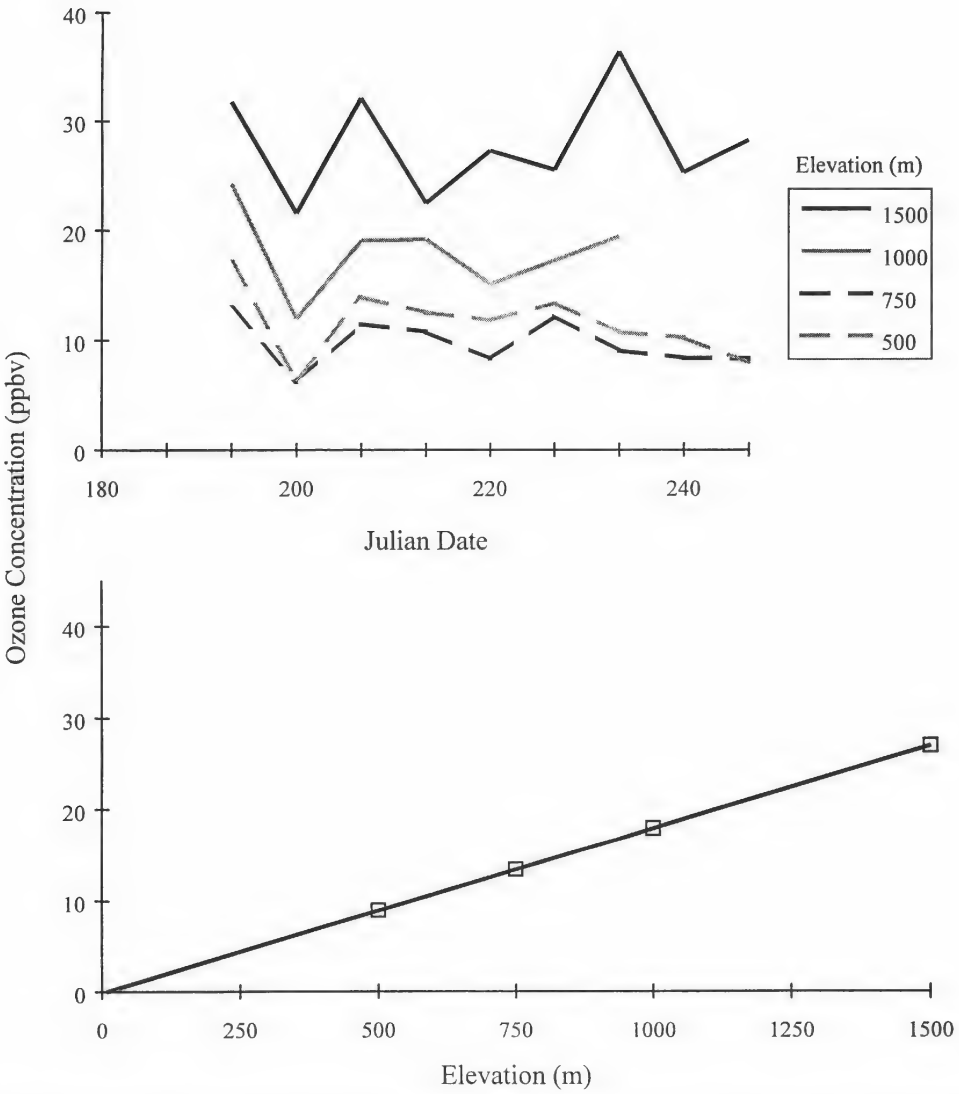

Figure 6. Weekly average ozone concentrations (upper graph) and seasonal averages of passive sampler data (lower graph) along an elevational gradient in the Soleduck River drainage, western Olympic Mountains, for the summer of 1996. These data, from a region with minimal air pollution, can be used as "reference" conditions for ozone at other locations.

component of the ozone measured in the Cascade Range is the result of atmospheric transport of anthropogenically-sourced ozone and ozone precursors from Seattle-Tacoma and other urban areas.

An indication of the relative quantity of anthropogenic ozone contributed to tropospheric ozone measured in the Nisqually drainage can be calculated by comparing the Nisqually data to a comparable "reference" site. Such a site is available in the western Olympic Mountains, specifically in the Soleduck River drainage, which receives westerly air flow from the Pacific Ocean and has minimal local pollutant sources. Ozone concentrations are extremely low here, even at

high elevations (Figure 6). If the Soleduck drainage is indeed a reference site, it should be possible to calculate anthropogenic ozone for the Nisqually drainage by "subtracting" the Soleduck data from the Nisqually data for sites of comparable elevation.

Using this approach, weekly average ozone concentrations over the course of a summer are approximately 12 ppbv higher along the Nisqually River than at the reference site. However, the highest weekly average ozone values on the Nisqually River are up to 43 ppbv higher than reference. These are reasonable estimates of the anthropogenic contribution and compare favorably with general estimates by Stockwell et al. (1997) of stratospheric and anthropogenic contributions to tropospheric ozone. Our findings are also corroborated by data from other sites (e.g., Steyn et al. 1997, Stockwell et al. 1997) and recent modeling results (Barna et al. In Press) that indicate that an increase in ozone above the reference level is caused by urban-based anthropogenic sources and subsequent dispersion.

A striking feature of the dataset is the similarity in temporal patterns of ozone concentration throughout the Nisqually transect. Visual examination of the time series of weekly average ozone concentrations reveals that for a given sampling date, there is a high degree of coherence between sites within transects and between transects (Figure 4). This is best seen by looking at the alignment of "peaks and valleys" in the time series from week to week. Although absolute ozone concentration may vary by elevation, relative concentration tends to be consistent. During periods of high ozone exposure, ozone concentrations tend to be high throughout the Nisqually drainage. This coherence in spatial and temporal ozone distribution has been found in other drainages of western Washington as well, and holds on a regional basis for the entire western half of the state (Cooper and Peterson In Press).

Conclusions

Mount Rainier National Park and other sites in the Cascade Range have higher average ozone exposure than urban areas to the west. The two highest-elevation sites at Mount Rainier have higher weekly average ozone concentration than any other site measured in western Washington (Figueroa et al. 1996, Cooper and Peterson In Press), a result of both anthropogenic inputs and a background ozone-concentration gradient increasing toward the stratosphere (Finlayson-Pitts and Pitts 1986).

Spatial and temporal distribution of ozone in western Washington exhibits strong coherence within the Nisqually drainage. The quantitative relationship between ozone and elevation (mean of 1.2 ppbv per 100 m of elevation gain) is similar to what has been measured throughout western Washington (Brace and Peterson 1998, Cooper and Peterson In Press). Therefore, in future monitoring efforts it may be reasonable to use this ozone-elevation relationship to estimate ozone distribution at mountain sites based on data from continuous analyzers or passive samplers at lower elevations.

Another dominant pattern is the strong synchrony in weekly average ozone concentrations between sites within the transect throughout the study period. The alignment of maximum and minimum weekly average concentrations over the Nisqually elevation gradient indicates that for any given week, relative ozone exposure is similar throughout the drainage even though absolute concentrations vary by elevation and longitude. Tropospheric ozone distribution in western Washington has a significant regional component (Cooper and Peterson In Press, Barna et al. In Press), with coherence in relative ozone exposure on a subregional basis (this study). Regional meteorological patterns likely contribute to atmospheric circulation and ozone synthesis at large spatial scales (Barna et al. In Press), while proximity to pollutant sources determines variation between river drainages. Elevation is a critical modifier of local ozone exposure and has a major impact on weekly average ozone concentrations throughout mountainous regions.

Because tropospheric ozone distribution in western Washington is affected by pollutant production, the physical environment, and meteorology at large spatial scales, it is imperative that regulatory agencies and natural resource managers consider a large-scale monitoring and air-quality management strategy. Currently, the monitoring network of continuous ozone analyzers is mostly at low elevations and within the greater Puget Sound metropolitan region. This monitoring focus on low elevations and urban areas is generally true throughout North America (Chameides

et al. 1997). However, limited analyzer data in rural areas (e.g., Böhm et al. 1991, Bytnerowicz et al. 1999) and data in this study indicate that both short-term (maximum hourly) and long-term (weekly average) concentrations are generally higher in mountainous and wildland areas downwind of urban areas. This has implications for the health of human populations in rural areas (Brauer and Brook 1997) and for vegetation that is sensitive to elevated ambient ozone (Peterson et al. 1992). Monitoring with an increased emphasis on quantifying ozone in rural areas would improve our understanding and protection of human health and natural resources on a broader spatial scale.

Our data suggest that tropospheric ozone distribution on the west side of Mount Rainier has such a strong subregional component that limited sampling can be done as long as the variation among sampling locations can be quantified. Despite some interannual variation, the consistent rate of ozone increase with elevation found in this study suggests that only one analyzer and perhaps one or two passive samplers are necessary to characterize average ozone exposure in the Nisqually drainage, because the ozone-elevation factor can be applied to calculate values for other elevations. In a previous study (Cooper and Peterson In Press), we showed that most of the Cascade Range drainages to the east of the Seattle-Tacoma urban core have similar ozone-elevation patterns. This suggests that limited sampling could be used to characterize multiple drainages within large subregions. While an expansion of the current monitoring network with continuous analyzers would provide an ideal approach for addressing regulatory concerns with respect to short-term, maximum concentrations, passive samplers are an inexpensive yet accurate technique for quantifying long-term exposure across a broad geographic area.

This study quantified spatial patterns of ozone exposure through intensive sampling of one river drainage for four summers. We feel that the spatial patterns observed are likely robust and can be used to guide future monitoring. Ozone exposure in the Nisqually drainage is similar to that of the Carbon River drainage to the north and higher than in drainages on the east side of the park (Brace and Peterson 1998). Furthermore, the Nisqually drainage is the most popular destination of recreationists in Mount Rainier National Park and contains several species of vascular plants with known sensitivity to ozone (Brace et al. In Press). For all of these reasons, continued ozone monitoring in the Nisqually drainage will optimize the detection of worst-case air quality as well as protection of human and biological resources in Mount Rainier National Park.

Acknowledgements

We thank Barbara Samora and John Ray for excellent scientific support and encouragement. Statistical consultation was provided by Loveday Conquest and Joel Reynolds. Stephanie Cooper assisted with data collection, Paige Eagle assisted with data analysis and graphics, and Robert Norheim created the map in Figure 1. Helpful comments on the manuscript were provided by two anonymous reviewers. Research was funded by Mount Rainier National Park and the National Park Service-Air Resources Division.

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Received 8 March 1999
Accepted 30 June 1999

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Characteristics of Young Forests Used by Spotted Owls on the Western Olympic Peninsula, Washington

Abstract

Although the dependence of spotted owls (*Strix occidentalis*) on older forests has been well documented, the specific attributes of comparatively younger forests used by owls have not been described in some regions. We collected habitat data at locations used by spotted owls tracked in an intensive radio-telemetry study to develop descriptions of these forests on the western Olympic Peninsula, Washington. After addressing the effects of triangulation error on the placement of our vegetation sampling plots, we collected data at all 16 telemetry locations that could be clearly associated with non-old-growth habitat, as well as 16 random locations. Owl locations were divided into 2 groups to reflect single-use (only one radio location within the error polygon) and multiple-use sites (≥2 radio locations within the error polygon) within home ranges. Vegetation data collected in three arrays of variably-sized plots included measures of stem and snag density (by diameter class), canopy cover, and cover of downed wood and shrubs. Our analyses indicated that single-visit and random locations did not differ with respect to the variables we recorded. However, both differed from multiple-use locations in abundance of larger snags, and amount of canopy closure. A logistic regression model indicated that multiple-use sites could be reliably distinguished from single-use and random locations based on the greater number of snags ≥51 cm diameter at breast height (dbh) and ≥70% canopy closure. Younger forests managed for spotted owl foraging habitat in this region should be in the understory reinitiation stage of stand development, have ≥70% canopy closure, and contain ≥4 snags/0.4-ha that are ≥51 cm dbh. The habitat definitions we propose may not be applicable to other areas characterized by different forest types and prey assemblages.

Introduction

Recent management and conservation strategies for the spotted owl (*Strix occidentalis*) on non-federal lands in Washington include passage of a state habitat protection rule (WAC 222-10-041; see WSFPB 1996), a proposed federal 4(d) rule (USDI 1995), and development of Habitat Conservation Plan (HCP) agreements between landowners and the U.S. Fish and Wildlife Service. Each of these strategies contains provisions for management of suitable habitats on non-federal lands. Specifically, the state rule provides regional descriptions of suitable habitats for spotted owls in Washington. In addition, the state rule and the HCP process allow for modification of habitat definitions based on new research information.

The definitions of habitats used for these management initiatives were derived from descriptions summarized by Hanson et al. (1993). Those descriptions were limited to submature forest types because it was felt that there was general agreement on the definition of old-forest habitat (Hanson et al. 1993). The information used by Hanson et al. (1993) to develop definitions of suitable habitat for the Olympic Peninsula was, in some cases, extrapolated from other parts of western Washington. Data from the western Olympic Peninsula were not readily available at that time although telemetry data had been collected in the home ranges of a number of owl pairs in that region (Forsman unpubl. data). That particular research was designed to estimate home range size and to investigate use of different forest types.

Although Forsman's research was not designed to describe specific habitat attributes within stands used by owls, we felt that it was important to describe the use of submature forest habitat(s) in the region based on conditions at sites known to have been used by spotted owls. The most reliable means to accomplish this was to examine habitat conditions at documented telemetry points

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(e.g. North and Reynolds 1996). Consequently, we collected habitat data at telemetry-based locations in submature habitats to address two objectives: 1) to provide a better description of non-old-forest habitat used by spotted owls on the western Olympic Peninsula, and 2) to test the null hypothesis that within-stand structural attributes of younger forests did not differ significantly among documented sites with single, multiple, or no documented records of use.

Study Area

We collected habitat data in two general areas on the western Olympic Peninsula in Washington where telemetry research had been conducted by Forsman: the vicinity of Forks in western Clallam County and the vicinity of Neilton in western Jefferson County. Both areas occur at the interface of the coastal lowlands and the foothills of the interior of the peninsula. The lowland region, dominated by state-managed and private lands, is of generally low relief whereas the foothills exhibit greater relief and are managed by the U.S. Forest Service and National Park Service.

The managed forests of the area are dominated by western hemlock (*Tsuga heterophylla*) although Sitka spruce (*Picea sitchensis*) and Douglas-fir (*Pseudotsuga menziesii*) are dominant in some areas. Other species, such as western redcedar (*Thuja plicata*) and Pacific silver fir (*Abies amabilis*), also occur in the area. Most suitable habitat on federal lands is typical old-growth forest (Mills et al. 1993, Forsman and Giese 1997) whereas suitable habitat on state and private lands occurs in a variety of conditions including: 1) young stands containing residual forest elements from stands largely destroyed by a catastrophic wind storm in 1921, 2) young stands which lack residual forest elements, and 3) remnant patches of old forest. Much of the nonfederal land area has been fragmented by timber harvests conducted in the last few decades.

Methods

Selection of Sampling Sites

The telemetry data were collected in 1987-1989 (Forsman unpubl. data). Most of the telemetry points represented nocturnal foraging locations of owls (n=10); a smaller number (n=6) were diurnal roost locations. The nocturnal points were determined by triangulation whereas the diurnal points were based on either triangulation or visual contacts of roosting owls. All independent telemetry points were subsequently placed on a map, digitized and entered into a database. Estimates of home range size and shape, used to identify the area within which random sampling would occur (see below), were made using the minimum convex polygon procedure (Hayne 1949).

To determine the stand location of mapped telemetry sites, we imported the digital data to a Geographic Information System (GIS) where they were overlaid on a series of orthophotos of the areas within the owl home ranges. We used these orthophotos and other maps of the study area to locate sites for sampling.

The inherent error associated with triangulation (White and Garrott 1986) made it necessary to develop a sampling scheme that addressed this potential source of bias. Forsman assessed the degree of triangulation error in the eastern Cascade Mountains in Washington and found a mean distance of 158 m between the estimated and actual locations of radio signals (E. Forsman, unpubl. data). We believe this error estimate was appropriate (and conservative) for the current study because the areas where we sampled habitat were characterized by less rugged terrain than the assessment study area; this may have resulted in a lower incidence of signal bounce. In addition, our study area was highly accessible due to a well developed road system, which made it possible to travel quickly to multiple points from which to receive radio signals required for triangulation.

Our goal was to sample habitat features in the vicinity (i.e., within the error polygon) of the telemetry locations and to compare with features at sites not known to be used by foraging owls within home ranges. We assumed that the area in the immediate vicinity of the mapped telemetry point was representative of the habitat being used by the owl at the time the radio signals were received. For this reason, we used a 316x316 m (10 ha) polygon (referred to below as a "cell") centered on the mapped telemetry point, to define the area within which we collected vegetation data. For consistency with our use of a grid of 10-ha squares to identify sites for random sampling, we used a square rather than a circular plot to represent the error polygon.

Our primary objective was to describe submature habitats used by spotted owls, so we rejected all telemetry points recorded in stands of old-forest habitat and those that we felt could reasonably be associated with nearby old-growth habitats. Given the possible magnitude of triangulation error that occurred in the collection of the telemetry data, we also rejected points that would result in erroneous sampling of unused non-suitable habitats. Therefore, we discarded all telemetry points that contained any of the following within the 316x316 error cell: 1) a stand or patch of more than 2 ha of old forest, 2) any amount of old forest that was contiguous with a stand or patch of old forest more than 2 ha in size outside the error cell, and 3) a stand or patch of less than 2 ha of suitable non-old-forest habitat in a cell otherwise comprised of non-suitable habitat.

Many of the stands were readily identified as old forest or non-suitable habitat and excluded based on our inspection of ortho-photos. However, habitat assessments of other stands required site visits. We defined any stand with an average of ≥ eight trees/0.4 ha of > 76 cm diameter at breast height (dbh) to be old forest, based in part on the definition used by the USFS in this region (Fierst et al. 1992a, 1992b). For this sampling strategy we considered any forest condition less than dispersal habitat to be unsuitable. Dispersal habitat was defined in part on the Washington State Forest Practices rules (WAC 222-10-041): stands with ≥70% conifer composition, ≥70% canopy closure, and ≥6.1 m open space between the top of the understory vegetation and the bottom of the live canopy.

Environmental conditions associated with forest edges are known to influence the composition and structure of forest stands in a zone associated with the edge area (Chen et al. 1992). Because a number of years had elapsed between the collection of telemetry data and our habitat assessments, we believed there was some potential for changes in edge conditions since the date of documented owl use. To minimize the effects of forest edge in our vegetation sampling, we did not sample vegetation within an interior stand buffer of 20 meters adjacent to gravel roads and 50 meters adjacent to clearcuts or stands of saplings.

We also collected data at random plots. We selected these sites by establishing a fixed grid of 316x316 m cells over the study area and randomly selecting cells from within the MCP home ranges. We collected data only at those random cells that met the conditions described above for sampling at the telemetry-based points. We collected data at a number of random cells equal to the number of telemetry-based points (i.e. $n = 16$).

Collection of Habitat Data

We collected data in three pairs of nested 0.1-ha and 0.8-ha plots at each telemetry-based point or randomly selected cell. One set of nested plots was centered on the point we identified as our best estimate of the actual telemetry location. We selected the plot center for the other two pairs of plots by randomly selecting two octants (i.e., northwest, northeast, southeast, or southwest) from the central point and placing the plots immediately adjacent to the central one in each of the two octants. At one site we repeated the random draw when one of the plots was too close to a forest edge. The data from the three plots at a point or in a cell were pooled in our analyses. Because one of our goals was to compare our data with the new Washington State Forest Practices rules (WAC 222-10-041) for spotted owls, we collected data using parameter categories based on values in those rules.

We used the larger 0.8-ha plot size to provide a greater area for measuring the abundance of certain uncommon features and measured more common features within the smaller plots (Spies and Franklin 1991, Buchanan et al. 1995). In the smaller (0.1-ha), more intensively sampled plot we tallied all trees in each of two dbh classes: 10-51 cm and 51-76 cm. We also tallied the number of snags 25-51 cm dbh and categorized them in one of three height classes (<5 m, 5-12 m, >12 m).

We measured canopy opening (the inverse of canopy closure) at the central point and at the plot edge in each octant in the smaller plots using a concave spherical densiometer (Lemmon 1956). To address concerns about the precision of single densiometer readings within a stand (Cook et al. 1995, but see Nuttle 1997) we recorded multiple estimates within each plot and then used the mean value of all plot measurements to represent the stand value. At each of these five points we recorded canopy opening in each of the four cardinal directions. Thus, we recorded a

total of 20 estimates for each of the three sampling plots in each stand.

We believed that estimation of total tree height would be difficult and potentially inaccurate due to the height of trees and the fact that limited visibility of the uppermost portion of the canopy would produce error in our estimates. For this reason, we measured the height to the base of the overstory canopy, using a clinometer, to provide an indication of the height of trees in the stand. The height to the base of the overstory canopy (hereafter referred to as "canopy base height") was defined as the height above ground to the lowest living branches that occur on at least three sides of the bole of a tree. We measured canopy base height on five dominant and/or co-dominant trees: the tree nearest to the plot center and the trees nearest to the perimeter of the 0.1-ha plot in each octant.

Small mammal prey populations of the spotted owl are believed to derive important resource benefits from downed wood and shrub cover components within the forest (Carey and Johnson 1995). We estimated the proportion of the ground covered by downed wood ≥2.4 m long and ≥10 cm diameter at the small end. Because of the difficulty in accurately estimating ground cover types over a 0.1-ha area, we estimated cover as either absent, <5%, or by increments to the nearest 10%. In some stands we noted that the coverage of downed wood in contact with the ground was lower than the cover of all downed wood which included those pieces not in contact with the ground. For this reason, we differentiated between the cover of downed wood in contact with the ground and the overall coverage. We included only the downed wood in decay classes I-IV (Sollins 1982) because they are distinctly identifiable as logs and could be measured. The proportion of ground covered by woody shrubs and conifer seedlings was estimated as none, <5%, or in increments of 10%.

In the 0.8-ha plots we tallied all trees ≥76 cm dbh and all snags ≥51 cm dbh. We used the same height categories for these large snags that we used above for the smaller snags.

Data Analysis

We analyzed the data set to determine whether there were differences in habitats among 3 categories of sites. The first category consisted of randomly-selected sites from which we had no documented use by spotted owls. The other two categories were sites consisting of single or multiple telemetry locations. We classified the latter sites by placing a 316x316 m error cell over the mapped location of the telemetry point and determining whether other telemetry locations occurred in the cell (multiple sites) or whether the cell was characterized by the single point. We collected vegetation data at only the first point location randomly selected within the cells with multiple locations (i.e., we did not double-sample within the 316x316 m cells).

Power analysis was conducted on preliminary data to determine the probability of failing to reject a null hypothesis that was false (a Type-II error), as suggested by Steidl et al. (1997). We collected data at 9 telemetry-based sites (5 single- and 4 multiple-location sites) to estimate sample size requirements necessary to achieve a desired level of statistical power ($\beta \leq 0.2$), following Hintze (1996). We used two variables well documented as important or potentially indicative habitat features for spotted owls: the number of large-diameter snags and the number of large-diameter trees. The analysis indicated $\beta < 0.1$ when $n = 5$ and $\alpha < 0.10$ in comparing the number of large trees at the single and multiple-point telemetry-based sites. Similarly, when comparing the number of large snags, we found that $\beta < 0.2$ when $n = 5$, and $\beta < 0.1$ when $n = 10$ (with $\alpha = 0.10$ for both). We concluded that our projected sample sizes were adequate for testing the hypothesis that these features are important to owls in younger/marginal habitats.

We assessed data distributions prior to statistical analysis. As expected in a sample of forest habitat data, many of the variables exhibited right-skewed distributions. In subsequent multiple-comparison analyses using generalized linear models (GLIM; Crawley 1993) a Poisson error distribution was incorporated in the ANOVA model. In situations where the data were over-dispersed (i.e., the data were not Poisson distributed), we used a scale parameter to approximate a negative binomial distribution (Crawley 1993). In GLIM, ANOVA models can be designed to compare all mean values against a specific mean, or reference value. We used this procedure for all three possible comparisons with each of two reference values (i.e., single- and multiple-point data

versus data from random sites, and multiple-point data versus single-point data).

We identified correlations among variables that were significant in the univariate analyses, and that might confound subsequent logistic regression (LR) analyses, by conducting Pearson correlation analyses for the three categories of site data. We excluded variables from the final analysis that were highly correlated ($P < 0.10$) with other variables. Finally, we used LR (Hosmer and Lemeshow 1989) to identify the combination of variables that best distinguished among sites used multiple times and those sites used once or not at all. A forward stepwise procedure was used to incorporate only those variables which significantly ($P < 0.10$) improved the model (Crawley 1993).

Results

We collected vegetation data at 16 independent telemetry locations, 11 in the Forks area and five near Neilton. Our sample included 8 sites with single relocation points and 8 sites with multiple relocation points. Overall, we sampled from the home ranges of four female and three male spotted owls.

Although we did not collect data on tree species composition, all stands we visited were dominated (e.g., ≥95% of stem count or basal area) by conifers, primarily western hemlock and Sitka spruce. The only variables that differed among multiple owl location sites, single owl location sites, and random cells were canopy opening (Table 1) and three measures of the abundance of large-diameter snags (Table 2). There was slight variability among other habitat features, but none of the differences were significant (Tables 1, 2).

Because there were no differences in vegetation features at single-location points and random cells, we combined those data and used LR to compare vegetation characteristics of those sites with the multiple-location sites. Due to significant correlations among some large snag variables, we chose a single variable, the abundance of large-diameter snags, that we felt was most biologically meaningful to include in the LR analysis. Only 2 variables were retained in the final LR model: 1) percent of canopy opening, and 2) abundance of large-diameter snags. The probability that a particular site was used multiple times by a spotted owl increased with an increase in the number of large-diameter snags and amount of canopy opening. The final LR model and associated parameter estimates of the probability of multiple use (PM) was:

$$PM = \frac{1}{1 + e^{5.283 - 0.110\,(\%\text{ canopy opening}) - 1.230\,(\text{number of lage snags})}}$$

with coefficient standard errors of 1.911, 0.062, and 0.527, respectively. The equation appeared to fit the data well, as indicated by a lack-of-fit analysis ($\chi^2 = 19.63$) and the Kappa statistic (0.667). Additionally, the model chi-square statistics (Afifi and Clark 1990) indicated that both variables were useful in sample classification (large-diameter snags: Wald $\chi^2 = 5.44$, $P = 0.020$; canopy opening: Wald $\chi^2 = 3.10$, $P = 0.078$). The probability that a site was used multiple times by a spotted owl was most strongly associated with the abundance of large-diameter snags (Figure 1).

The logistic regression model correctly classified six of eight (75%) multiple-location sites and 22 of 24 (92%) single-point and random sites. The overall correct classification rate was 88%. The two incorrectly classified multiple-location

TABLE 1. Mean (±SE) values of habitat characteristics recorded at random sites (i.e., no documented use; $n = 16$ cells) and those sites used by spotted owls as determined by radio-telemetry (both single and multiple telemetry locations; $n = 8$ sites for each) on the western Olympic Peninsula, Washington. Habitat variables are reported on a per 0.4-ha basis.

Variable	Use Category			F Statistic	*P*
	Random Location	Single Location	Multiple Location		
No. 10.2-50.7 cm trees	238.6 (23.00)	257.0 (47.60)	197.3 (30.41)	0.726	0.493
No. 50.8-76.1 cm trees	23.1 (4.95)	21.2 (6.41)	38.2 (7.52)	1.632	0.213
No. trees (all dia. classes)	263.4 (20.00)	279.4 (42.40)	238.9 (27.40)	0.409	0.668
Canopy base height (m)	16.9 (1.07)	16.4 (1.49)	19.6 (1.02)	1.594	0.220
Canopy opening (%)[1]	6.2 (1.04)a	10.9 (2.17)a	14.4 (4.47)b	3.982	0.030

[1] Variables with different letters were significantly different.

TABLE 2. Median (with 25% and 75% quartiles) values of habitat characteristics recorded at random sites (i.e., no documented use; n = 16 cells) and those sites used by spotted owls as determined by radio-telemetry (both single and multiple telemetry locations; n = 8 sites for each) on the western Olympic Peninsula, Washington. We report median values in this table because these data were not normally distributed. Habitat variables are reported on a per 0.4-ha basis.

Variable	Use Category			F Statistic	P
	Random Location	Single Location	Multiple Location		
No. ≥76 cm trees	0.9 (0.04, 2.5)	0.6 (0.04, 2.7)	3.9 (1.2, 4.8)	2.235	0.125
No. 25-51 cm snags, 2-5 m tall	0.0 (0.0, 1.0)	0.0 (0.0, 2.3)	0.0 (0.0, 1.0)	0.538	0.590
No. 25-51 cm snags, 5-12 m tall	0.0 (0.0, 1.3)	0.0 (0.0, 2.3)	0.7 (0.0, 2.3)	0.385	0.684
No. 25-51 cm snags, ≥12 m tall	0.7 (0.0, 1.3)	2.0 (0.0, 4.0)	0.7 (0.0, 2.7)	0.841	0.442
No. 25-51 cm snags, all heights	1.3 (0.0, 3.7)	4.0 (0.7, 6.0)	2.0 (0.3, 6.0)	0.490	0.618
No. ≥51 cm snags, 2-5 m tall	0.2 (0.0, 0.3)a	0.3 (0.04, 0.3)a	1.6 (0.8, 2.7)b	18.050	0.00001
No. ≥51 cm snags, 5-12 m tall	0.0 (0.0, 0.1)a	0.1 (0.0, 0.3)a	0.7 (0.3, 2.1)b	9.838	0.0006
No. ≥51 cm snags, ≥12 m tall	0.6 (0.3, 1.1)	1.1 (0.4, 1.6)	1.4 (1.0, 2.5)	1.215	0.311
No. ≥51 cm snags, all heights	0.8 (0.3, 1.9)a	1.3 (0.9, 2.3)a	3.8 (2.5, 6.9)b	9.445	0.0007
Downed wood in contact with ground (%)	7.5 (5.0, 12.1)	3.8 (2.5, 9.4)	5.0 (3.1, 6.9)	1.190	0.319
Total downed wood (%)	7.5 (5.0, 16.0)	6.3 (2.5, 10.6)	5.0 (5.0, 9.4)	0.477	0.625
Shrub cover (%)	8.3 (2.5, 31.5)	10.0 (3.8, 32.5)	5.8 (2.9, 25.8)	0.327	0.723

[1] Variables (within a row) with different letters were significantly different.

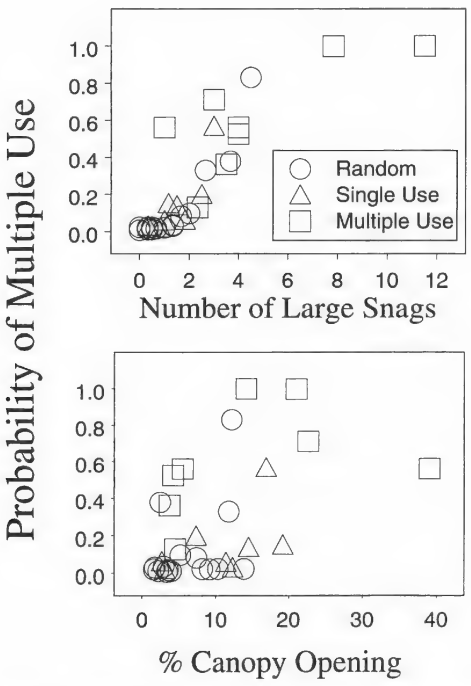

Figure 1. Relationship between probability that a site was used multiple times by a spotted owl and the abundance of large-diameter snags/0.4-ha (top); although a significant component of the final model, the relationship between owl use and amount of canopy opening was not as strong (bottom).

sites appeared to have been misclassified because of low measures of canopy opening (4% canopy opening in both cases). Conversely, the incorrectly classified single-point and random locations had greater canopy opening (12% and 17%). All four misclassified sites had between 2.3 and 4.5 large-diameter snags per 0.4 ha.

Discussion

Our results suggested that the abundance of large-diameter snags and the amount of canopy closure are important habitat components that distinguish among submature (SM) and young forest marginal (YFM) habitats used by spotted owls in the western Olympic Peninsula. The snag and canopy opening values at multiple-location and single-point/random sites were similar to SM and YFM habitats, respectively, as defined in the rules. For this reason, we compared the data from this study to those definitions, and make recommendations as to how local definitions might be modified in accord with local information.

The current Washington State Forest Practices Rules define SM habitat as a conifer-dominated stand (≥30% conifer) with ≥70% canopy closure, 115-280 trees (≥10 cm dbh) per 0.4 ha, ≥3 snags per 0.4 ha of ≥51 cm dbh and at least 5 m in height, and optional provisions for using other correlated attributes (WAC 222-16-085-1[b]). The definition for YFM habitat differs in that the snag requirement is ≥2 snags per 0.4 ha and the cover of

downed wood and shrubs is ≥10% and 25-60%, respectively (WAC 222-16-085-1[b]). According to our model, a stand of SM habitat (on our study area) with 3 large snags (≥51 cm dbh) and 30% canopy opening (70% canopy closure) would have a 0.85 probability of being used multiple times by spotted owls. Reducing the amount of canopy opening to 10% or 0% results in lower probabilities of multiple use (0.61 and 0.20, respectively). This suggests that efforts to open dense stands through silvicultural manipulations (i.e., commercial thinning) may improve habitat quality and benefit spotted owls.

The biological significance to spotted owls of large-diameter snags has long been recognized in the Pacific Northwest (Forsman et al. 1984). These snags are used as nest sites by spotted owls (Forsman et al. 1984, Forsman and Giese 1997) and are an important habitat element, particularly in terms of denning and resting sites for their primary prey, the northern flying squirrel (*Glaucomys sabrinus*; Carey et al. 1997). Our results suggest that SM habitat is typified by, among other things, the presence of ≥4 large-diameter (i.e., ≥51 cm dbh) snags/0.4 ha ≥5 m in height. Nearly one-half of these large-diameter snags were ≥12 m in height. Relatively short snags (2.4-4.9 m) were more abundant on multiple-use sites compared to single-use sites, suggesting a possible value of these structures to spotted owls. The abundance of the shorter snags may, however, be correlated with other attributes that more strongly influence owl use of these stands (e.g. possibly the number of large snags ≥12 m in height); additional work is needed to investigate the biological importance of these structures.

Our data on forest community composition and percent canopy opening were consistent with existing habitat definitions (e.g. Hanson et al. 1993). With only one exception, the stands we visited had <30% canopy opening (≥70% canopy closure). The greater canopy opening in the multiple-location sites appeared to be related to greater structural complexity of the stands. Specifically, the multiple location stands had greater canopy opening, more large-diameter snags, and tended to have fewer stems, all indications of the understory reinitiation stage of stand development (Oliver 1981).

The range of stem densities we noted in stands used by owls (Table 1) was greater than previously recommended for this region (115-280 stems/0.4 ha; Hanson et al. 1993). Specifically, 2 of the 8 (25%) multiple-use locations had more than 280 stems/0.4 ha, but only 4 (13%) of the 32 telemetry-based or random sites had stem counts >380/0.4 ha. For this reason, we suggest that the upper limit of acceptable stem density is about 380 stems/0.4 ha ≥ 10 cm dbh for the western Olympic Peninsula. A component of the total stem count was the abundance of 51-76 cm trees; the differences among site categories for this diameter class (and the relatively low *P* value), although not significant, suggest potential selection by owls. A retrospective power analysis suggests that additional investigation is warranted to evaluate the possible importance of this habitat attribute (e.g. data from 80 sample plots would be required, with power of 0.80 and $\alpha = 0.10$, to detect a 50% change in the density of 51-76 cm trees found at random plots).

Downed wood and shrub cover are believed to be important components of spotted owl habitat by providing cover and other resources for small mammal prey (Carey and Johnson 1995). We found that the amounts of downed wood and shrub cover in the stands were variable, and that overall the mean amount of cover did not differ among the categories of sites. Furthermore, the mean amounts of downed wood and shrub cover we recorded were lower than the lower limit required in the Forest Practices rules (WSFPB 1996). Our data suggest that 5% cover of downed wood might be appropriate for defining the lower threshold of this component of spotted owl habitat. Similarly, a lower range in shrub cover (e.g. ≥10%) may be warranted. We recognize, however, that these values represent only what the owls in our study used on average, and may not reflect optimal conditions for prey species in SM habitats (Carey and Johnson 1995).

Certain limitations apply when using telemetry data to make inferences about habitat quality. One of the primary concerns in this type of analysis is that the recorded occurrence(s) in an area may not reflect the actual ecological value of the site (North and Reynolds 1996; see Van Horne 1983). In the context of our study, this means that there may be situations where owls use a site to a greater or lesser degree than is indicated by telemetry data. There are many possible reasons for this, including sampling problems related to

the number of telemetry locations or the timing or frequency in which they were collected, and ecological factors such as occupancy of the study area by unknown conspecifics, other competitors, or predators. In this study we used telemetry data collected from resident, reproductive owls that were intensively monitored (302-462 locations/owl) during all seasons of the year (13-23 months/owl; Forsman in prep.). We have no way to evaluate whether the ecological factors above influenced the habitat use we observed, although such influences likely occur in all natural populations. Therefore, we believe that the telemetry sampling results represented variations in intensity of use and were adequate for our purposes.

Although we believe the data reported above confirm and refine our understanding of habitat attributes used by spotted owls in this region, caution is warranted. Our primary objective was to compare the attributes at telemetry relocation sites in lower-quality habitats with those at random locations. We defined the lowest-quality habitats used by the spotted owls in this study, but further research in an area, which includes a wider successional range of habitats, may better define the lower limit of habitat suitability for spotted owls. Moreover, we believe it is important to distinguish between regulatory definitions of habitat and those used for conservation purposes. Regulatory definitions represent thresholds to facilitate identification of sites or stands where an assessment, typically to evaluate potential impacts, may be required. For conservation planning purposes, however, we believe that the higher values of attributes found in our study (e.g. ≥4 large snags/0.40 ha) are more appropriate because they reflect habitats that the owls appear to use to a greater extent than YFM. Habitats that are used to a greater proportion than their availability (e.g. mature and old forest seral stages; Forsman, unpubl. data) are generally thought to have greater value than habitats used less than or equal to their proportional availability.

Acknowledgements

We thank Don Saul, John Talmadge, and Shelly Snyder for their efforts to develop a variety of home range and triangulation error polygon maps that were compatible with the orthophotos we used. Janet Anthony, Julie Rivers, Dave Manson, Bernard Shroeder, and Camille Speck collected the vegetation data, and Bruce Casler, Sue Grayson, Martha Jensen, Timm Kaminski, Kevin Maurice, Doreen Schmidt, Stan Sovern, and Margy Taylor collected the telemetry data. Jim Bleck, Karen Holtrop, David Kenney, Lowell McQuoid, Beth Naughton, Kathy O'Halloran, Theresa Powell, and Dan Varland provided logistical or other support in the field. We also thank Anita McMillan and Jack Smith for their support, and Mary Gobel, Kathleen House, Jackie Likes, and Tom Owens for assistance with data management. John Skalski assisted with project design and made comments that improved the manuscript. We thank Jason Karl and D. Erran Seaman for making constructive comments that improved the paper.

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Received 13 January 1999
Accepted 16 August 1999

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The Encroachment of Exotic Herbaceous Plants into the Olympic National Forest

Abstract

A floral survey in the Olympic National Forest and its surroundings revealed that a considerable number of introduced ruderal plant species have made deep inroads into the stands of native flora. Some of them, which are mainly of European and Asian origin, have been planted deliberately to stabilize the soil along roadsides and after clear cutting and burning. However, they have already established reproductive communities that are capable of spreading rapidly without additional human help, as they have already done in almost all regions of the earth subject to a temperate climate. Plotting the data from the Geographical Information System, it was shown that 12% of an area totaling 388 km^2, located mainly in the Olympic National Forest, was occupied totally or in large part by this mainly ruderal flora, which accounted for at least 50% and usually nearly 100% of all plants within the area on which they occurred. This represents a major qualitative and quantitative biogeographical alteration in the regional flora of a national forest generally considered to be only slightly affected by human activity.

Introduction

A phytogeographical process initiated by the wanderings of human beings has been changing the world's flora throughout recorded history, but for the past century, this process has been accelerated at an alarming rate. It has resulted in the formation of new floral aggregations, recruited mainly from Europe and Asia and transported to biotic communities located on all continents except Antarctica (Hitchcock & Cronquist 1973; Weihe 1972). In many places, these species have been intentionally planted, whereas in others, they arrived as contaminants of seed. Once established on a continent, they often spread rapidly because of their great potential for massive seed dispersal (Baker 1974). The result has been the formation of ruderal communities throughout the temperate zones of the world from subtropical and Mediterranean to sub-arctic regions. The formation of these communities has been facilitated by anthropogenic alterations of the vegetation, particularly those related to housing, road building, and leisure activities. These exotic species have been augmenting and even displacing endemic floral aggregations on an ever growing area of the earth's surface (Wilgen and Richardson 1985; Kowarik, 1995). As pointed out by De Ferrari and Naiman (1994), even the widespread interest in this phenomenon has resulted in relatively few studies on a landscape scale. However, the problem of exotic plants in the State of Washington has been drawing a considerable amount of public attention. A list of the introduced species first reported in the state from 1950 to 1996 and a discussion of the role some of them have assumed has been provided by Toney et al. (1998).

The purpose of this study was to determine the structure of the biotic communities in which the introduced species develop, estimate their present quantitative impact in the coastal forest on the Olympic Peninsula of Washington, and provide a synopsis of the history of its development and spread. It must be emphasized that these communities are fundamentally different from those which were formerly encountered in the local ruderal habitats. It is an aggregation of international origin rather than native. The spread of the species is progressing at an extremely rapid pace, especially in the Pacific Northwest of North America. For example, only 40 species of non-native plants had been identified on the Olympic Peninsula prior to 1900, and 143 before 1936 (Jones 1936). By 1995, 333 non-native species, accounting for 25% of the flora, were found on the Olympic Peninsula (Buckingham et al. 1995). However, many of the same exotic ruderal species, mainly from Europe, are presently encountered in such places as Japan (Kitamura et al. 1987), Australia, New Zealand, and South Africa (Weihe 1972), as well as in North America. Previous ecological studies that have provided information on the exotic flora of the Olympic Peninsula have focused on the forest succession (Fonda 1974) and those species penetrating the forest along the courses of

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the Dungeness and Hoh Rivers (De Ferrari and Naiman 1994). There have also been studies that concentrated mainly on communities of native plants in the Olympic Mountains (Fonda and Bliss 1969; Henderson et al. 1989), as well as the general flora of the region, cited above. This study, conducted mainly in the Sol Duc River Valley, focuses on the importance of roads, particularly the many unpaved logging roads, as avenues of invasion. It is the first attempt to evaluate the quantitative impact of the present management practices conducive to the introduction and spread of the foreign ruderal species on the landscape.

Location

The spread of the international ruderal vegetation was analyzed in and at the edges of the Olympic National Forest in western Washington, U.S.A. The quantitative spread of these ruderal species was determined in the northern part of the forest, which is drained mainly by the Sol Duc River (Figure 1). Although such a study could have been made almost anywhere in the temperate zones, the location along the Pacific Coast in northwestern North America is of special interest because the native flora is typically dominated by conifers, ferns, mosses, lichens, and other vascular plants that are especially adapted to the conditions in cool rainforests or moist coastal forests. Very few of the native species show the adaptations similar to those of the exotic ruderal plants, as discussed below, and only a few of the ruderal species are likely to have reached the Pacific Northwest without human assistance. Clear lines of demarcation between the invading and natural flora were observed at the start of the study, and these are described in detail below (Structure of the Ruderal Aggregations).

Material and Methods

The cartography of the vegetation was completed using recent aerial photos of the Sol Duc River Valley and parallel ridges in or adjacent to the Olympic National Forest. The regional vegetation was observed on the ground, and the structure of the various plant communities was determined.

Figure 1. The location of the site surveyed (black rectangle) on the Olympic Peninsula in the State of Washington.

The species present along transects at least 10 m wide through the forest and along various roads and streams were determined. The locations of the species aggregations on the areas covered by the maps were then plotted according to the findings made during the field survey. Care was taken to visit all of the distinct zones observable in the photos, including mature forest, replanted forests in various stages of development, clearcuts, lands used for agriculture or animal husbandry, roadsides, the riparian zone along streams, and the vicinity of buildings. Surveys were also made along logging roads reaching to the top of the ridges located within the area surveyed. Only gardens around private houses were omitted form the survey, because the amount of the area covered by such gardens was insignificantly small, and many of the plants growing in them are not viable in natural communities. The presence of the ruderal vegetation either alone or interspersed with other plant aggregations on cleared areas was then plotted on the map, and the number of square meters it covered was calculated on the horizontal plane of the maps. By this method, some underestimation of the area it covered is possible because areas on hillsides are actually greater than they appear on the maps. The area of all unpaved roads with a strip 1 m wide along each side as well as a 5 m area on each side of Highway 101, which transects the area surveyed, was added to the total. The paved area of the highway was not included in the total area inhabited by ruderal vegetation. This may also result in an underestimation of the area occupied by ruderal plants because they usually cover much more than 5 m on each side of the main roads and more than 1 m along minor logging roads. The area of unpaved roads themselves was included in the total because the ruderal plants often grow in the middle of them.

A total of 388.2 km^2 was surveyed using aerial photos that had been taken in 1994 and digitized as data in a Geographic Information System (GIS). The approximate percentage cover of the total area largely dominated by herbaceous plants predominantly belonging to the exotic ruderal community was calculated using the program ArcView™ by marking all bare areas and cut woodlands in early stages of regeneration together with the marginal strips along all roads. Field surveys were conducted by walking the transects during the spring and summer of 1998, noting the species present 5 m on each side of the way, and photographing the vegetation to confirm the presence of the ruderal species on these areas.

It was further determined that only a few additional forested areas had been cleared of trees since the GIS data were obtained in 1994, and these were still only partially colonized by plants, with many areas still bare of nearly all vegetation. The charts prepared were compared with those produced to map the seral stages of the native vegetation during previous years and stored in the GIS in order to provide an additional check of the accuracy of the mapping. The data used for comparison were obtained from an unpublished forest service report on the Sol Duc Pilot Watershed Analysis by Mr. David Peter. The program ARC/INFO™ was used to calculate the area of the region surveyed on which the ruderal flora occurred at the time the aerial photos were taken.

Results

Structure of the ruderal aggregations

While walking along the transects, it became apparent that the exotic ruderal species generally form aggregations that exclude native herbaceous species along roadsides and similar disturbed areas (Table 1). In undisturbed forests dominated by the species listed in Table 2, it was usually found that no exotic species were present. From these observations and from photographs made in the region, it became evident that the majority of the area has either 100% or 0% coverage by exotic species.

Mixtures of exotic and native species are encountered along a narrow ecotone between ruderal roadside communities and undisturbed forest. These characteristically appear as grasses invading stands of forest floor vegetation. Other mixtures of native and introduced species are present on clearcut areas. It was observed that after the trees are removed, most of the shade-adapted plants of the forest floor quickly succumb to dryness and strong illumination. However, thick stands of the sword fern [*Polystichum munitum* (Kaulf.) Presl.], are able to persist for long periods of time among the encroaching exotic herbs, which are usually intentionally seeded on the clearcuts to prevent erosion. These remain as the only representatives of the native herbaceous flora, but they also gradually disappear with time. On the Olympic Peninsula, the woody plants that

TABLE 1. Species of the ruderal vegetation that colonize areas of the Olympic Peninsula disturbed by man and the geographical origins of the component species. The distribution of the individual species in ruderal habitats is influenced locally by such factors as the amount of moisture present and the amount of shading by adjacent forests. However, deliberate seeding of the roadsides and clearings cut in the forest is still a primary factor determining where the species will be encountered. Most identifications were made using Hitchcock & Cronquist (1973), but the nomenclature was updated to follow that of Buckingham et al. (1995). The superscript after the name refers to the first report of the species on the Olympic Peninsula, according to Jones (1936) and Buckingham et al. (1995).

Species	Probable origin
Pteridophyta	
Equisetum arvense L.[1]	North America, Europe
Dicotyledonae	
Achillea millefolium L.[2]	North America, Europe, Asia
Anaphalis margaritacea (L.) Bentham & Hooker[1]	North America, Europe, Asia
Barbarea verna (Mill.) Ascherson[4]	Europe
Barbarea vulgaris Robert Brown[4]	Europe, Asia
Bellis perennis L.[3]	Europe
Calystegia sepium (L.) Robert Brown[3]	Europe
Capsella bursa-pastoris (L.) Medicus[2]	Europe, Asia
Chrysanthemum leucanthemum L.[3]	North America, Europe, Asia
Cirsium arvense (L.) Scopoli[3]	Europe
Cirsium edule Nuttall[1]	North America
Cirsium vulgare (Savi) Tenore[3]	Europe
Digitalis purpurea L.[2]	Europe, Asia
Epilobium angustifolium L.[1]	North America, Europe, Asia
Erodium cicutarium (L.) l'Héritier[4]	Europe, Asia
Gnaphalium uliginosum L.[4]	Europe, Asia
Heracleum lanatum Michaux[1]	North America, Siberia
Hieracium aurantiacum L.[4]	Europe
Hypericum perforatum L.[3]	Europe, Asia, North Africa
Hypochaeris radicata L.[2]	Europe
Lactuca muralis (L.) Fresenius[3]	Europe
Lapsana communis L.[3]	Europe, Asia
Lathyrus latifolius L.[4]	Europe
Lotus pedunculatus Cavanilles[4]	Eurasia, Africa, Australia
Lysimachia punctata L.[4]	Europe, Asia
Lythrum salicaria L.[4]	Europe
Medicago lupinula L.[3]	Europe, Asia, North Africa
Melilotus officinalis (L.) Lamarck[4]	Europe, Asia
Myosotis arvensis (L.) Hill[3]	Europe, Asia, North Africa
Plantago lanceolata L.[2]	Europe
Plantago major L.[2]	Europe
Polygonum cuspidatum Siebold & Zuccarini[4]	Japan
Polygonum sachalinense Schmidt[4]	Eastern Asia
Prunella vulgaris L. var. *vulgaris*[4]	Europe
Ranunculus acris L.[3]	Europe
Ranunculus repens L.[2]	Europe
Rumex acetosella L[2].	Europe
Rumex crispus L.[2]	Europe, Asia
Sagina procumbens L.[3]	Europe
Senecio jacobaea L.[4]	Europe
Solidago canadensis L.[1]	North America
Sonchus oleraceus L.[3]	Europe, Asia
Taraxacum officinale F.Weber ex Wiggers[2]	Europe, Asia
Trifolium hybridum L.[3]	Europe

Table 1 continued, next page

Species	Probable origin
Trifolium pratense L.[2]	Europe, Asia
Trifolium repens L.[2]	Europe, Asia, North Africa
Vicia sativa L.[2]	Europe, Asia, North Africa
Monocotyledonae	
Agrostis capillaris L.[4]	Europe, Asia, North Africa
Agrostis stolonifera L.[4]	Europe
Avena fatua L.[4]	Europe, Asia, North Africa
Bromus hordeaceus L.[4]	Europe
Dactylus glomerata L.[2]	Europe, Asia
Elymus glaucus Buckley[1]	North America
Elymus trachycaulus (Link) Gould[4]	North America
Holcus lanatus L.[4]	Europe, Asia, North Africa
Holcus mollis L.[3]	Europe
Juncus balticus Willdenow[1]	North America, Europe
Juncus bufonius L.[1]	North America, Europe, Asia
Juncus effusus L.[1]	North America, Europe
Lolium perenne L.[2]	Europe
Phleum pratense L.[2]	Europe, Asia
Poa trivialis L.[4]	Europe, Asia, North Africa
Vulpia myuros (L.) C.C. Gmelin[4]	Europe
Vulpia octoflora Walter[1]	North America

[1]A probable native species (Jones, 1936),
[2]Introduced prior to 1900,
[3]Not reported before 1900 but known to have been introduced prior to 1936,
[4]Not known to have been introduced until after 1936.

develop on cleared areas are generally native, but the spread of exotic woody plants, such as Scots broom, [*Cytisus scoparius* (L.) Link], can be expected in the near future.

To illustrate the structure of the vegetation typically encountered while walking through areas subjected to human influence, a transect from the middle top to middle bottom of Figure 2 can be taken. Beginning at the bottom, a roadside aggregation is encountered in which nearly 100% of the herbaceous plants are exotic, but surviving sword fern tufts are occasionally scattered among the ruderal vegetation.

In contrast to the herbaceous plants, the woody vegetation consists of 100% native species at most locations. Surviving vine maples, *Acer circinatum*, and species of *Rubus* are particularly characteristic of the region. Near the edge of the deciduous trees at the bottom of the picture, a narrow ecotone is encountered, in which there is a mixture of native and exotic herbaceous plants. Beneath the trees themselves, the native species gain the upper hand and account for well over 50% of the species present. Moving out of the trees onto the clearcut at mid-level in the photo, another ecotone is encountered, followed by an area on which almost 100% of the herbaceous species are exotic. Rarely, isolated edible thistles (*Cirsium edule*) occur among the exotic species in the clearcuts, but non-native thistles are more abundant. In the clearcut shown, there is a seasonal succession involving exotic grasses, the common foxglove (*Digitalis purpurea*), scattered composites, clovers (*Trifolium* spp.), and docks (*Rumex* spp.). In addition to the exotic herbaceous species, a few native woody species and small native conifers can also be found.

Moving beyond the road in Figure 2, a closed section of forest is encountered. While about 100% of the herbaceous plants along the roadside are exotic, those under the forest canopy are nearly 100% native. There is a very narrow ecotone at the edge of the forest in which there is some mixture of native and exotic species. In summary, the transect through this photograph (Figure 2) runs through unshaded areas in which nearly 100% of the herbaceous plants are exotic, through closed canopy forest in which little more than 0% of the herbaceous plants are exotic, and through narrow ecotones and open canopy woods in which there

TABLE 2. The most abundant native plant species dominating the climax stage forests in the region surveyed and their native ranges. Pacific Northwest refers to the Pacific Watershed of North America and adjacent Rocky Mountains.

Species	Native Range
Trees	
Acer macrophyllum Pursh	Pacific Northwest
Alnus rubra Bongard	Pacific Northwest
Pseudotsuga menziesii (Mirbel) Franco	Western North America
Tsuga heterophylla (Rafin) Sargent	Pacific Northwest
Thuja plicata D. Don	Pacific Northwest
Woody vegetation in understory and edges of clearings	
Acer circinatum Pursh	Pacific Northwest
Oplopanax horridus (Smith) Miquel	Northern North America
Rubus parviflorus Nuttall	Western North America
Rubus spectabilis Pursh	Pacific Northwest
Sambucus racemosa pubens (Michaux) House	North America
Herbal understory growth	
Claytonia cordifolia (Watson) Pax & Hoffmann	Western North America
Cornus unalaschkensis Ledebour	Pacific Northwest
Listera caurina Piper	Western North America
Lycopodium clavatum L.	Circumboreal to tropics
Oxalis oregana Nuttall	Pacific Northwest
Pteridium aquilinum (L.) Kuhn	Cosmopolitan
Bryophtyes	
Hyloconium splendens (Hedwig) Bruch,Schimper, & Gümbel	North America, Europe, Africa, New Zealand
Hypnum circinale Hooker	Pacific Northwest
Isothecium stoloniferum Bridel	Western North America
Kindbergia oregana (Sullivant) Ochyra	Pacific Northwest
Polytrichum juniperinum Hedwig	Cosmopolitan
Rhizomnium glabrescens (Kindberg) Koponen	Western North America
Rhytidiadelphus loreus (Hedwig) Warnstorf	North America, Europe
Thuidium recognitum (Hedwig) Lindberg	Northern Hemisphere

is some mixture of native and exotic species. The newly logged side of the hill in the upper left quarter of the figure is almost bare of vegetation. The native understory plants have died off since the logging, and the exotic plants have only recently begun to move onto the clearing.

The introduced ruderal plants observed during the field study are shown in Table 1. A number of additional alien species were reported for the Olympic Peninsula by De Ferrari and Naiman (1994) and Buckingham et al. (1995). The majority of the species originated in northern Europe and have spread throughout many parts of the temperate zones (Weihe 1972). Some of them are native to eastern Asia. A few are thought to have been present in North America since prehistoric times, and some of these have apparently been introduced to the Pacific Northwest from other parts of the continent during recent human migrations.

Spread of the exotic ruderal species

The field surveys during spring and summer showed that the ruderal plants are virtually the only vegetation along most roadsides, encroach extensively into the clearcuts in the forest, and share the areas with plants of subsequent seral stages until the conifer forests have almost completely regenerated. Along numerous transects through the forests, none of the species in Table 1 were ever encountered on the floor of intact, mature forests or along unmodified streams, but

Figure 2. Hillsides near the site of the survey in Clallam County showing typical closed forest and clearcut areas. A transect through the center of this photo from top to bottom reveals the "all or none" nature of exotic species aggregations in the local herbaceous flora. In contrast, the woody plants belong almost exclusively to native species. For details, see text.

they persisted on unused roads and former clearings that had been fully overshadowed by young conifers.

A simplified map showing the Sol Duc River and the locations occupied wholly or predominantly by the ruderal community, which consists almost exclusively of species that have become pan-temperate, is provided in Figure 3. A planimetric analysis of the map indicates that a total of 45.935 km^2 are occupied by that community. which equals 11.8% of the total area of the region covered by the photos. Because the region surveyed lies mainly within a national forest and is uninhabited, this percentage of land on which the native flora of herbaceous plants has been replaced almost entirely by species introduced from other continents is considerable. It should also be remembered that this large area does not include parts of forest and woodland in which a few exotic species are encroaching among the native forest floor species. Such encroachment can be expected to occur most frequently along streams and rivers and on natural clearings. In the inhabited parts of the Olympic Peninsula, a much greater percentage of the flora is accounted for by this pan-temperate ruderal community because the ruderal community is also promoted by agriculture.

The ruderal community is clearly a primary seral stage that is gradually displaced as the sere progresses. The plants are useful for stabilizing the soil on cleared areas. For this reason, they are frequently planted intentionally, which has contributed to their rapid colonization of such large areas in the region. The introductions of plants, however, has not always had benign results. Much effort is currently being devoted to eradicate the Scot's broom, which has become a very troublesome weed since its introduction. Several introduced herbaceous species are poisonous to domestic animals. For example, the tansy ragwort (*Senecio jacobaea*) produces alkaloids that are toxic to horses and cattle (Whitson et al. 1991), and expensive eradication programs to eliminate it have been proposed. The meadow buttercup (*Ranunculus acris*) is also poisonous to cattle (Parish et al. 1996). The area already colonized by the ruderal community is considerable, so

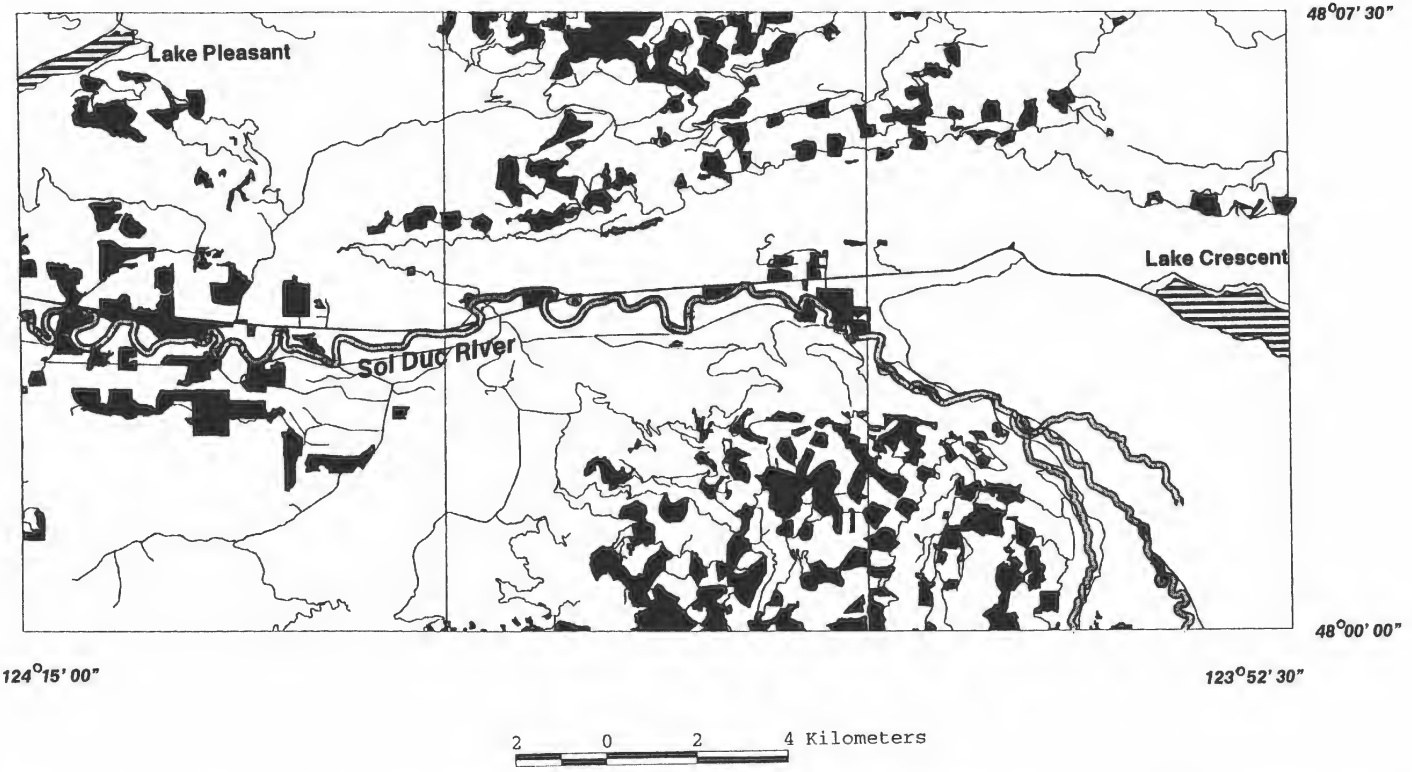

Figure 3. The area of 388.25 km^2 surveyed during the study with the subareas occupied wholly or to a large degree by ruderal flora shown in black. The double black lines outline the Sol Duc River, while the narrow lines indicate roads along which the ruderal plants grow. On this map, the area occupied by the herbaceous ruderal flora, which consists nearly 100% of exotic species, is at least 45.935 km^2 or 11.83% of the total.

judging from the fact that these species had not reached the region at all until the late 19th or early 20th century, the present extent of their coverage represents a major floral change in the Pacific Northwest region of North America.

Discussion

History of floral change

The encroachment of the pan-temperate ruderal community, mainly of European origin, into the Pacific Northwest is typical of a process that has been taking place throughout the temperate zones, mainly during this century. The pan-temperate ruderal community has spread rapidly with the systems of highways and logging roads and is presently altering the flora of the temperate zones in North and South America, Asia, and Australia, to various degrees, as demonstrated by the range information on the individual species, provided by Weihe (1972). The native plant aggregations of the rainforest region on the Olympic Peninsula of Washington are strikingly different in structure and ecological characteristics from those along the edges of the deciduous forests of Europe (Moravec et al. 1982), where much of the ruderal vegetation has had its origin. Table 2 provides a short list of some of the dominant native plant species of the forests on the Olympic Peninsula, which were characterized by Franklin & Dyrness (1973) as being mainly old growth forest, dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) and notable for the dense epiphytic flora. In addition to the abundant mosses (Schofield 1992), which coat much of the forest floor and the tree trunks, the vegetation is characterized by a particularly large variety of lichens (McCune & Geiser 1997). For this reason, the demarcation lines between the introduced community (Figure 4) and the native flora (Figure 5) are recognizable at a glance. In eastern North America, there is less distinction between the native and non-native vegetation because many of the introductions occurred well

Figure 4. A typical ruderal community in the middle of a little used dirt road during the late spring. The dominant species in this aggregation are *Trifolium repens* and *Bellis perennis*.

Figure 5. A native forest floor community of late spring dominated by *Linnaea borealis* and *Cornus unalaschkensis* Ledeb. that occupies open ground at the edges of roads and clearings before it is overgrown by the faster-growing introduced species.

over a century ago, and many species have already integrated themselves with the native flora (Fernald 1987). Sharp ecological demarcation lines are no longer apparent between New and Old World species. However, the encroachment of the ruderal plants has been no less dramatic.

The floral changes involving the ruderal species are still more significant for phytogeography than for economics, although this may change dramatically at any time. The ruderal species are considered to have a positive effect in holding the soil in place wherever human activity has stripped away the natural vegetation. Usually, native vegetation is able to displace the ruderal species during the course of the natural sere. However, introductions of some plant species, mainly those that become established in pastures, are having some severe economic effects because of their toxicity to domestic animals (Whitson et al. 1991; Parish et al. 1996), as mentioned above. The rapid growth of the introduced species works to the disadvantage of any native ruderal species present in the region. In the Pacific Northwest, the redwood sorrel (*Oxalis oregana* Nutt.), wild strawberry (*Fragaria virginiana* Duchesne), sweet-scented bedstraw (*Galium triflorum* Michx.), little buttercup (*Ranunculus uncinatus* D. Don.), red columbine (*Aquilegia formosa* Fisch.), Cooley's hedge-nettle (*Stachys cooleyae* Heller), and the twinflower (*Linnaea borealis* L.), which is a circumboreal species (Dempster 1993), are frequently observed in partially shaded locations at the edge of the forest along roads. However, the results of the observations along the transects confirmed that these are rapidly overgrown whenever the introduced ruderal species, particularly the grasses, begin to colonize the habitat. Figure 2 shows areas being rapidly overgrown by ruderal plants, and at these sites, no native ruderal species were ever observed. It can be assumed that prior to the coming of the first European settlers, the entire region provided few areas for

colonization by ruderal herbs, so the native species had little chance to develop varieties well adapted to this kind of habitat. One of the only ruderal species that has apparently been established on the Olympic Peninsula since prehistoric times is the field horsetail, (*Equisetum arvense*), which is still an abundant ruderal species is moist locations (Hauke 1993). However, it is nearly pantemperate in distribution and was apparently already present on several continents prior to the Quaternary Period (Hauke 1993), when the retreat of the glaciers permitted it to colonize the region now known as western Washington (Jones 1936).

As the sere progresses, these first stage species, some of which are encountered in sunny places on the forest floor, have been overgrown by native species of the next seral stage, mainly woody shrubs, such as the salmonberry (*Rubus spectabilis*) and thimbleberry (*Rubus parviflorus*). However, the native species of the second seral stage are being increasingly displaced by another European introduction, the Scot's broom. This displacement threatens to have economic consequences because simple efforts to eradicate the rapidly spreading import are proving unsuccessful, and more elaborate methods will probably be employed, which will be expensive but probably will not be effective, either. Unlike the ruderal herbs, the Scot's broom is thought to be capable of stopping the growth of young conifers.

The final seral stages are still dominated by native species, which eventually overshadow the sun-loving ruderal species and eliminate them from the area. However, Figures 2 and 3 show that with increasing human activity in the forest, the stands of native climax vegetation are increasingly fragmented into isolated stands surrounded by introduced species. The roads are particularly effective at dissecting the native forests, and they provide avenues of penetration that take the ruderal floral aggregations new to the region deep into the forest.

At the present time, the area occupied by the ruderal community, 11.83% of the total area surveyed, is enough to cause concern. This is particularly true because the advance of these species along the many small roadways in the forest permits this exotic vegetation to dissect the native forests into disjunct islands of conifers and their natural understory plants. This is a remarkable floral change considering that during the first half of the 19th century, the Olympic Peninsula was settled only by native Americans, whose hunting and fishing societies caused only minimal change to the forest. Settlement of the region by persons of European descent began only during the second half of the 19th century and progressed slowly. The floral changes in the region apparently began to accelerate considerably during the first half of the 20th century, and the advance of the ruderal community with the roads did not take place with any great speed until the second half of the century. As already discussed, Jones (1936) found that there had been a considerable augmentation of the non-native flora between 1900 and 1936. Since that time, the introduction of exotic species has intensified considerably (Buckingham et al. 1995). Judging from the trends that have taken place during this century and the time required for introduced species to become invasive (Kowarik 1995), nonnative species can be expected to bring about fundamental changes in the flora of the Olympic Peninsula during the next few decades.

Along the Dungeness and Hoh Rivers to the south, De Farrari and Naiman (1994) reported that 28% and 24%, respectively, of the plant species present were exotics. They discussed the role of these rivers as invasion routes for the introduced plants, confining their discussion mainly to natural dispersion and accidental transport of seed. In the Sol Duc Valley, however, the roads seem to be the main avenues of transport, and deliberate seeding of roadsides and clearcuts makes discussion of other dispersal mechanisms moot.

Outlook

Although there are presently few obvious dangers to the native flora due to invasive spreading of the introduced species, problems are sure to arise in the future. Kowarik (1995) was able to trace the development of introduced species in Brandenburg for a period of more than two centuries. In the case of woody plants, he noted that an average of 147 years elapsed between the introduction of species and the time they became invasive. He further found that it is not possible to predict which species will become troublesome for the native vegetation. Even if we assume that invasiveness will manifest itself among herbaceous plants more rapidly than among woody

species, decades may elapse before one of the newcomers begins to develop into a dangerous competitor of the native species. Several of the species in Table 1 seem to have the potential to become invasive. For example, Edwards et al. (1995) noted that the purple loosestrife (*Lythrum salicaria*) has a tendency to spread rapidly and form monospecific stands in other parts of North America. This shows that considerable trouble with the species already introduced can be expected during coming decades, and new exotic species are still being brought to the Pacific Northwest for landscaping purposes by both the timber industry and private groups ostensibly attempting to manage the environment. At the present time, a clear separation of communities of exotic species and those of native species is maintained because the exotic species are adapted to strong illumination, while the native plants are overwhelmingly adapted to the shade on the forest floor. The development of shade-tolerant populations of invasive exotic species is all that is necessary to open the way into the forest, permitting the new species to compete directly with the natives. It is time that attention be given to the serious consequences that can occur due to the introduction of foreign species for erosion control or to beautify the environment.

Acknowledgements

Special thanks are due to colleagues in the United States Forest Service Forest Sciences Laboratory at Olympia, Washington. Mr. David Thysell provided considerable help in identifying and confirming the identifications of many native and introduced plant species and for critically reading the manuscript. Mr. Rick Jordan was kind enough to print out the first two figures from the GIS system and calculate the areas occupied by the roads and clearings using the program ARC-View. Funding for the study was provided by the Pacific Northwest Research Station of the U. S. Forest Service.

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Received 2 February 1999
Accepted 16 August 1999

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Effects of Outboard Motor Emissions on Early Development of the Killifish *Oryzias latipes*

Abstract

Two stroke outboard engines produce large quantities of combustion emissions per liter of fuel consumed. To determine the environmental risk of outboard motor emissions (OME) to the early life stages of fish, we exposed killifish (Medaka), *Oryzias latipes*, embryos to water contaminated with OME . Time for larval development, incidence of larval abnormalities, and larval mortality all increased, and length of hatched larvae decreased, with exposure to increasing concentrations of OME-contaminated water. Chemical analysis using solid phase extraction, followed by gas chromatography, indicated high concentrations of polycyclic aromatic hydrocarbons in the OME water. Application of these results to hypothetical lakes suggests significant risks to fish development in the case of high OME input rates to small lakes.

Introduction

Two-stroke outboard engines are common, yet inefficient, power sources for boats of many kinds. Because these engines combine fuel intake and combustion in the same stroke, some of the incoming fuel-air mixture passes uncombusted through the cylinder. Gases are emitted into the atmosphere and solubilized along with unburned fuel directly into the water (Jackivicz and Kuzminski 1973a). Because of this inefficiency, two-stroke outboard engines are currently being examined as major contributors of hydrocarbons to the environment. Hydrocarbons emitted from outboard engines represent approximately 30% of the total emissions from off-road vehicles (U.S. EPA 1996a). Two-stroke outboard motors produce approximately 200 to 300 g of hydrocarbons per liter of fuel combusted (Tjarnlund *et al.* 1996). Pleasure boats exhaust 1.59 x 10^9 liters (420 million gallons) of unburned gasoline and other hydrocarbons into U.S. waters each year – a volume equivalent to 40 Exxon Valdez-size oil tanker spills (Mele 1993).

Polycyclic aromatic hydrocarbons (PAHs) are common constituents of combustion emissions and are known carcinogens and mutagens (Neff 1979). They can cause changes in behavioral patterns, growth and reproduction in marine organisms (Connell and Miller 1984). Outboard motor emissions (OME) contaminated water can, in high concentrations, have toxic effects on a variety of adult fish species (Tjarnlund *et al.* 1996). However, little is known about the effects of PAH emissions from outboard engines on embryonic and early life stage development of fish (Jackivicz and Kuzminski 1973b).

Until recently outboard engines were not subject to emission regulations (Mele 1993). However, beginning in December, 1997 the U.S. EPA imposed air pollution standards on recreational watercraft. Tighter standards will be phased in over a period of ten years and will result in more efficient, cleaner-burning, direct fuel injection engines. Nevertheless, with an estimated 120 million two-stroke outboard engines currently in use in the United States (Mele 1993), the PAHs emitted into aquatic environments will likely remain substantial.

Because of the known toxicity of PAHs to aquatic life (Payne *et al.* 1988, Connell and Miller 1984, Neff 1979), we hypothesized that OME would adversely effect the development of fish larvae. We investigated the effects of OME-contaminated water on the development of killifish (Medaka), *Oryzias latipes*. We also measured the PAH content of the OME-contaminated water, and applied our laboratory findings to assess the environmental risk to lakes.

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Methods

Exposure Water

We collected water 1 to 2 days prior to our exposure experiments, from Pass Lake, Fidalgo Island, Washington, which is a relatively pristine lake where outboard engine use is prohibited. A 1968 Evinrude model 3836 three horsepower, two-stroke outboard engine with a fuel mixture of regular unleaded gasoline and two cycle motor oil (50:1) was used for the study. To determine if outboard emissions could cause any toxic effects in the test organism and to define a range of outboard emission concentrations to be used in a definitive experiment, we conducted a pre-test. The outboard engine was operated at medium throttle in a polyethylene tank containing 129 L of lake water for 30 minutes. This volume of water and run time was chosen simply for convenience. Based on toxicity test results from the pre-test (below), we decided to use a 60 minute run time and same volume of water (129 L) in the definitive experiment. To determine fuel burned, the fuel tank was weighed before and after operation. The control and OME contaminated waters were filtered through a 750 µm mesh nitex screen to remove large particles. The control (untainted lake) water was used to dilute the OME water to six water soluble fractions (WSF)-100%, 80%, 60%, 40%, 20%, 0%. To prevent fungal and bacterial growth methylene blue dye was added to each dilution at a concentration of 0.1 ml L^{-1}.

Toxicity Test

We used the killifish *Oryzias latipes* as a test organism because it readily reproduces in the laboratory, has been used in many toxicological studies, and the developmental stages of the transparent embryo have been well documented. Embryos are 1.5 mm in diameter. The larvae are 4 to 5 mm in length at hatching, which occurs in about eleven days at their optimum temperature of 25 °C. They begin feeding about 24 h after hatch (Kirchen and West 1969). We obtained healthy killifish embryos, approximately 29 h post-fertilization, from Carolina Biological Supply Co. and exposed them to 10 ml of each WSF in 15 ml Corning sterile polystyrene cell well plates. The wells were placed in a 25 ± 1 C incubator with a twelve h light:dark cycle (Kirchen and West 1969).

In the pre-test, to define a range of OME concentrations to use in toxicity tests, we exposed only one embryo per WSF concentration. In the definitive test, to better define the dose response, we used six embryos per WSF concentration. To establish a well-defined baseline 12 embryos were used per control. All results presented are based on the definitive test.

Daily observations of the embryos were made with a dissecting microscope at 16x, 25x, and 40x. We recorded data on heart rate, pigmentation, fin and organ development, and movement. Death was determined by the absence of a heartbeat. Developmental stages (Kirchen and West 1969) were noted until approximately 125 h post-fertilization. Within 8 h post-hatching, the larvae were preserved in 5% formalin and within 7 days larval length was measured using an IBM-PC Optimas program and a Sony VCC Video camera, calibrated to a Wild 16x lens.

Chemistry

Outboard motor emissions water (100% water-soluble fraction, WSF) was analyzed using U.S. EPA Method 525 (Supelco 1995, Eichelberger *et al.* 1988). Solid phase extractions were performed using Supelco Inc. ENVI™-18 cartridges and J.T. Baker® Ultra-grade resi-analyzed toluene and methanol. Each column was conditioned with 2 X 6 ml of toluene:methanol (10:1) followed by 6 ml methanol and 6 ml nanopure H_2O. Ten ml of 100% WSF were extracted at 3 to 4 psi and a flow rate of 5 ml min^{-1} followed by 15 min of air to dry the sample. Samples were eluted with 2 X 1 ml of toluene:methanol (10:1) and refrigerated at 3 to 4°C for approximately 24 h prior to analysis. Samples were analyzed using a Hewlett-Packard 5890 gas chromatograph. Sample solvent blanks and a standard solution containing 10 ppm of 16 different PAHs were run under the same conditions and used to identify and quantify unknown peaks present in the OME samples.

Results

Toxicity Test

After 211 h of exposure, all control embryos had hatched. Delayed hatching was observed in the higher WSFs (Figure 1). Delays in embryo development were evident as early as 18.5 h after initial exposure to OME water (45.5 h post-fertilization). Final

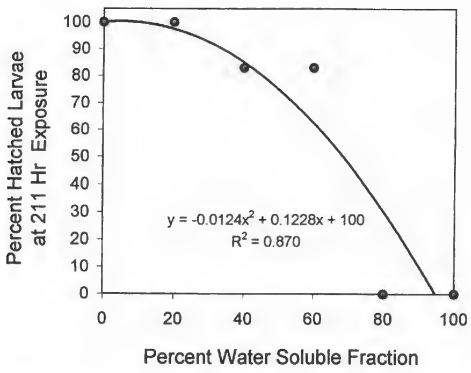

Figure 1. Relationship between % WSF of OME and % larval hatch after 211 hours exposure.

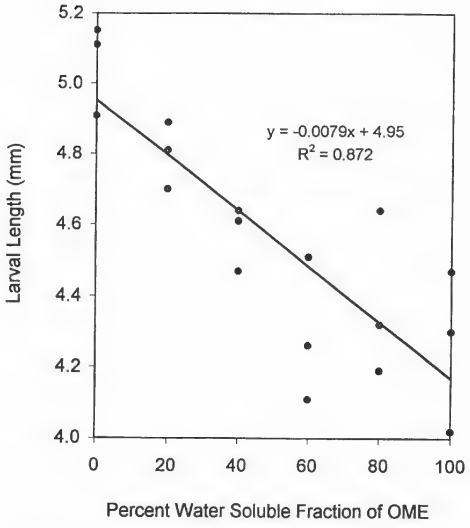

Figure 2. Larval length decreases with increasing WSF.

hatch time in 80% WSF was 353.5 hours post-exposure, i.e. 142.5 hours later than complete hatching in the 0% WSF.

Numerous morphological abnormalities occurred in embryos or larvae exposed to OME (Table 1). Effects included underdeveloped or abnormal eyes, absence of spleens or swim bladders, spinal abnormalities, underdeveloped hearts, and mortality. In WSFs of 60% or greater embryonic eyes lacked visible pupils. Spleens, easily visible in the control fish, were frequently absent in larvae exposed to 20% or greater WSF (Table 1). Kyphosis (abnormal spinal curvature) occurred in 50% of embryos exposed to 40% or greater WSFs. In addition, irregular or slowed heart rates were observed in water-soluble fractions (WSFs) of 60% and higher. The length of newly hatched larvae decreased with increasing WSFs of OME (Figure 2). At 172 h, 17% of embryos in 60% WSF died (Table 1) and overall mortality increased with an increasing percent WSF (Figure 3).

Chemistry

After operating the engine, the tank water had a strong odor of oil and gasoline, appeared cloudy, and was tan in color. The solvents eluted from the cartridges in two phases and the top organic layer was run through the gas chromatograph. Despite this phase separation, recovery of PAHs from the standard solution was 90% or greater with low background noise in the untainted water sample.

TABLE 1. Percentage embryo/larval abnormalities following exposure to different water soluble fractions (WSF) of outboard motor emissions. For each WSF n=42, ND=no data

	Percent Water Soluble Fraction of Outboard Motor Emissions					
Abnormality	0	20	40	60	80	100
Dead prior to hatching	0	0	0	17	ND	67
Dead following hatching	0	0	0	ND	100	33
Abnormal heart	0	0	17	17	83	100
Loss of blood color	0	0	17	50	100	100
Abnormal swimming	0	17	0	83	ND	ND
Curved spine	0	0	50	50	83	ND
Abnormal eyes	0	17	0	100	ND	67
Absence of swim bladder	0	0	50	67	ND	ND
Absence of spleen	0	33	83	83	ND	ND

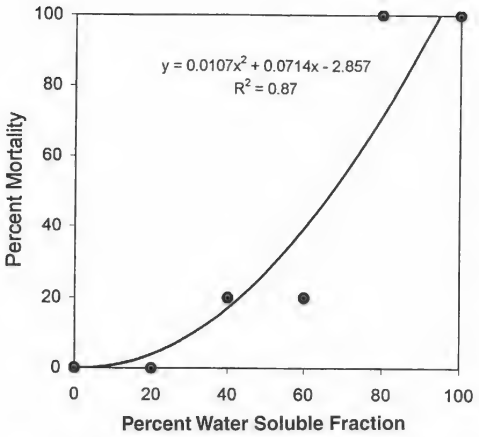

Figure 3. Percent larval mortality increases with increasing WSF of OME.

The OME samples contained numerous highly concentrated PAHs. Because of the complexity of the mixture and overlapping peaks, only four specific PAHs were identified in the OME water: Naphthalene (N), Acenapthene (A), Benzo-[k]fluoranthrene (BkF), and Benz[a]anthracene (BaA). Concentrations of PAHs in the 100% WSF were 180 to 5000 mg L^{-1} (Figure 4).

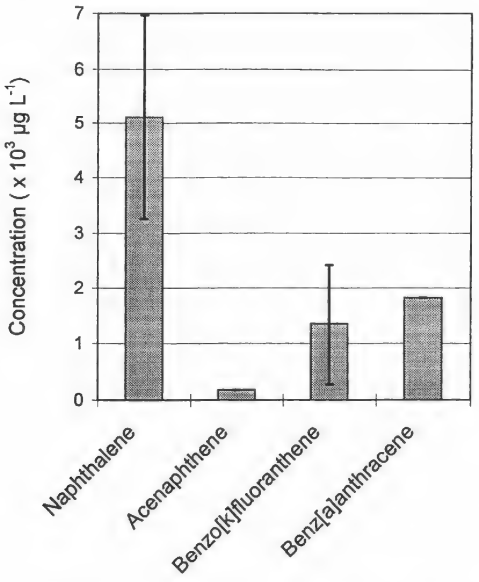

Figure 4. Four PAHs and their concentrations in 100% WSF.

Discussion and Environmental Risk

We found numerous adverse developmental effects in killifish exposed to outboard motor emission (OME) water. Our data clearly indicate a delay in development time of embryos exposed to OME water at all water-soluble fraction concentrations. Levels of PAHs in the 20% or greater WSFs undoubtedly account for the mortality at hatching and other adverse effects observed in our study. Assuming similar compound solubility, observed effects would be at concentrations of about 1000 µg L^{-1} N, 360 µg L^{-1} BaA, 280 µg L^{-1} BkF, and 36 µg L^{-1} A. Other studies report biological effects at similar concentrations. For example, naphthalene is toxic to pink salmon fry at 920 µg L^{-1} (Neff 1979), and soluble aromatic derivatives are lethal to marine larval stages at concentrations of 100 to1000 µg L^{-1} (Connell and Miller 1984). Acenaphthene at a concentration of 608 µg L^{-1} causes 50% mortality in the early-life-stage of fathead minnows (Cairns and Nebeker 1982).

Chemical products of outboard motor emissions have been found in aquatic environments. Trace constituents of outboard motor oils and exhausts (certain C27 to C35 pentacyclic terpanes) were found in the plankton of Conception Bay, Newfoundland, Canada (Bieger et al. 1996). Little information exists on concentrations of PAHs in lake water. Concentrations of total PAHs were .025 to 0.234 µg L^{-1} in Lake Constance Germany (Borneff and Kunte 1964) and.005 µg L^{-1} in Lake Erie at Buffalo, New York (Basu and Saxena 1978).

Hydrocarbons of low solubility, including PAHs, accumulate in surface films (the aquatic surface microlayer) where they reach high concentrations (Hardy 1987, Hardy and Cleary 1992). These films pose a threat to surface-living and surface-feeding organisms (neuston) (Hardy et al. 1987) and, through wind and current patterns, deposit on beaches (Gardiner 1992).

Furthermore, shoreline residents on some lakes draw their drinking water directly from the lake. The U.S. EPA has established drinking water standards for only a few PAHs (EPA 1996b). For benzo[a]pyrene (BaP) the EPA standard is 0.2 µg L^{-1}, and in Washington State the standard for groundwater is 0.008 µg L^{-1} (WAC-173-200-040[2]). For napthalene, the drinking water equivalent level (DWEL) is 100 µg L^{-1}.

The PAH concentrations found in our study resulted from one small (3 horsepower) outboard engine burning 0.5 liters of fuel in a 129 L tank. What might be the effects of multiple engine emissions on fish development in a real lake? The concentration of PAHs in lake water resulting from outboard emissions will be the result of many interacting factors, but can be approximated as follows:

PAH μg L^{-1} lake water = [(number engines)(average use h day^{-1})(L fuel consumed $engine^{-1}$ h^{-1})(μg soluble PAH produced L^{-1} fuel consumed)(residence time of PAH, days)] / (lake volume L)

Using this model, we predict resultant PAH concentrations and fish larval toxicity based on several scenarios of boat use and lake volume, assuming negligible inflow/outflow dilution (Table 2). Fuel consumption for outboard engines differs greatly, but for a moderate-sized engine we assume 30 liters h^{-1}. In Table 2, quantities of PAH emitted L^{-1} fuel consumed are based on our chemical analytical results. Lifetimes of PAHs are derived from the literature. For example, PAHs are biodegraded in natural waters with half lives of from 0.5 to 20 days (naphthalene) and 57 to 529 days (benzo[a]pyrene) (Howard et al. 1991). The turnover time of PAHs in a controlled ecosystem is 10 days for naphthalene and 1400 days for benzo[a]pyrene (Neff 1979).

As indicated (Table 2), with 60 outboards, averaging 8 hours per day on a lake of 1 x 10^{10} liters volume, no toxic effects on killifish larvae or on drinking water criteria for napthalene would be expected. Thirty-five outboards on a lake of 1 x 10^9 liters, or less would result in napthalene concentrations exceeding EPA drinking water criteria, but would not likely be toxic to killifish larvae. However, the same 35 outboards on a very small (1 x 10^8 L) lake would exceed drinking water criteria for napthalene and would also be toxic to killifish larvae (based either on napthalene or benzo[k]fluoranthrene concentrations). These estimates do not include the possible additive or synergistic effects of the many other PAHs and chemicals resulting from OME emissions.

In summary, our results suggest that moderate use of two-cycle outboard motors on large lakes poses little or no threat to water quality. However, heavy use of such motors on small lakes with low inflow/outflow dilution could result in PAH concentrations great enough to inhibit early life stage development in some fish. Also, on some lakes PAHs from outboard motors could threaten drinking water quality.

Acknowledgements

This work was supported by the National Science Foundation, Research Experience for Undergraduates Program Grant #OCE-9424050. We thank Terry Meredith, Scientific Technical Services, Western Washington University for assistance with PAH analysis and Gene McKeen Western Washington University's Shannon Point Marine Center for logistical and mechanical support.

TABLE 2. Scenarios of lake contamination from outboard motor emissions.

	Contaminant					
	napthalene			benzo[k]fluoranthrene		
Lake volume (L)	1.00E+10	1.00E+09	1.00E+08	1.00E+10	1.00E+09	1.00E+08
Number engines on lake	60	35	35	60	35	35
Average use (hours day-1)	8	8	8	8	8	8
Fuel consumption rate (L engine-1 h-1)	30	30	30	30	30	30
Soluble PAH (μg L-1 fuel consumed)[1]	1.29E+06	1.29E+06	1.29E+06	2.80E+03	2.80E+03	2.80E+03
Residence time of PAH (days)	10	10	10	1400	1400	1400
Resulting PAH concentration (μg/L)	19	108	1084	6	33	329
Exceeds toxic level for killifish larvae[1]	no	no	yes	no	no	yes
Exceeds EPA Drinking Water Criteria[2]	no	yes	yes	NA	NA	NA

[1]Our data

[2]DWEL Drinking Water Equivalent Level. A lifetime exposure concentration protective of adverse, non cancer health effects, that assumes all exposure to a contaminant is from a drinking water source.

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Received 19 March 1998
Accepted 7 September 1999

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Habitat Selection by Female Black Bears in the Central Cascades of Oregon

Abstract

Public scrutiny over management of black bears (*Ursus americanus*) in Oregon resulted in the passing of a referendum to ban the use of dogs and bait to hunt bears in 1994. Challenges to bear management necessitate the application of regionally derived biological information to bear management. The overall objective of this research was to define habitat characteristics that influence the autecology of female black bears in Oregon. Because habitat-selection processes operating at finer resolutions (e.g., the home range) are inevitably the product of landscape characteristics, we chose to study selection at both the home range and landscape scale. We radio-tracked 14 adult female black bears from June 1993 to December 1995 in the central Cascades of Oregon to determine home-range size and analyze habitat selection. Locations were classified to one of six habitat classes based on stand structure, and digitally overlaid onto a habitat map produced from a LANDSAT Thematic Mapper scene of the study area. A geographic information system was used to determine habitat characteristics at known and random locations; chi-square and logistic regression techniques were used to analyze habitat use. Female black bears were associated with open-canopy sapling/pole and open canopy mature timber, apparently selecting for a combination of foraging opportunities and security cover. Furthermore, black bears were negatively associated with roads and positively associated with streams. Consequently, roads located along watercourses may inhibit the use of riparian areas by bears. Understanding how forest-management practices influence the availability and use of habitats for black bears, and applying this knowledge to bear-management strategies, will ensure that management plans are based on the best available science, and confer greater credibility to state agencies from an increasingly informed and involved public.

Introduction

Managed as a game species under the authority of the Oregon Department of Fish and Wildlife (ODFW), the black bear population in Oregon was estimated at 25,000 animals statewide (ODFW 1992). In recent years, black bear management has become increasingly controversial, culminating in a public referendum in 1994 that banned the use of dogs and bait to hunt black bears. Challenges to bear management underscore the necessity of using the best available information to formulate black bear management guidelines. In addition to demographic data, maintaining viable black bear populations requires information on black bear ecology. Specifically, understanding how female black bears interact with their environment is important because habitat quality and quantity affect reproductive potential (Pelchat and Ruff 1986, Reynolds and Beecham 1980).

Information on habitat use by black bears in Oregon is limited (Barber 1983, McCollum 1973). Although data on habitat use obtained from studies in adjacent western states is somewhat applicable to Oregon (Beecham 1983, Lindzey and Meslow 1977, Poelker and Hartwell 1973), the composition of black bear habitat may differ considerably among states with varying vegetation communities. We studied home ranges and habitat use of female black bears at two scales by use of radio telemetry between June 1993 and December 1995 on the Willamette National Forest in the central Cascades of Oregon. The overall objective of this study was to examine habitat use of black bears in a managed forest. Specific objectives were to: (1) determine home-range sizes of female black bears; (2) compare habitat characteristics of known locations to random locations generated within home ranges; (3) compare habitat use and availability of habitats within home ranges; and 4) compare habitat use and availability within the range of the study-area population.

Study Area

This research was conducted near Oakridge, Oregon on the Rigdon Ranger District of the

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Willamette National Forest (Figure 1). The study area was located on the western slope of the Cascade Mountain Range and encompassed approximately 134,500 ha. Most of the area, with the exception of the adjacent Diamond Peak Wilderness, was extensively managed for timber production and supported an extensive road network. Clearcutting, the predominant logging method, produced a matrix of regenerating timber stands typically < 45 years old interspersed with

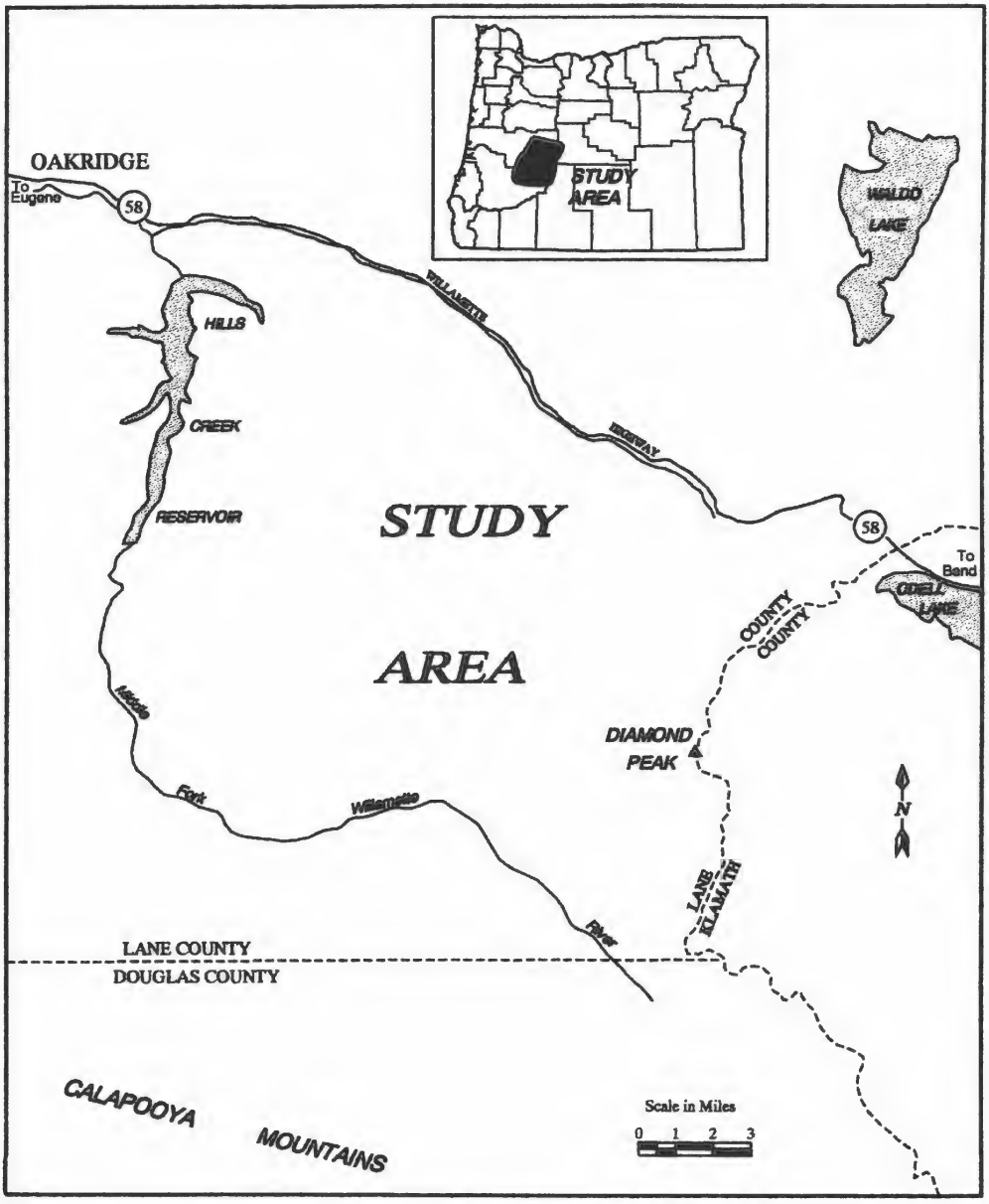

Figure 1. Location of female black bear study in the central Oregon Cascades, 1993-1995.

unmanaged forest > 80 years of age. In September 1988, an arson fire (the Shady Beach Burn) burned 3,708 ha of forest; much of the burned timber was subsequently clearcut resulting in extensive areas of grass-forb habitat surrounded by mature forest characterized by numerous canopy gaps and snags.

Study area elevations ranged from 460 m to 2,460 m at the summit of Diamond Peak. Most ridgetops were approximately 1,300 m. The topography was highly dissected due to glaciation and stream erosion, and was extremely rugged (Hemstrom et al. 1987). Two major watercourses, Hills Creek and the Middle Fork of the Willamette River, drained the area. Annual precipitation ranged from about 114 cm to over 178 cm on the higher ridges. Snow below 900 m was transient and drought conditions in summer were common. Temperatures ranged from approximately -12 C in winter to highs near 38 C in summer.

Dense stands of Douglas-fir (*Pseudotsuga menziesii*) dominated dry, low-elevation sites (Franklin and Dyrness 1973) and quickly regenerated in canopy gaps. Moist, low-elevation forests (below 1,000 m) consisted primarily of the western hemlock (*Tsuga heterophylla*) series. Higher elevations (900 m to 1,500 m) were dominated by the Pacific silver fir (*Abies amabilis*) series including Douglas-fir, western hemlock, and mountain hemlock (*Tsuga mertensiana*). Grassy openings on south slopes contained manzanita (*Arctostaphylos columbiana*) and Pacific madrone (*Arbutus menziesii*). Common understory species found throughout the area included Oregon grape (*Berberis nervosa*), salal (*Gaultheria shallon*), rhododendron (*Rhododendron macrophyllum*), and several species of huckleberry (*Vaccinium* spp.).

Methods

Bear Captures

We captured female black bears in Aldrich foot snares (Flowers 1977) in spring 1993-1995, and immobilized them with tiletamine hydrochloride and zolazapam (Gibeau and Paquet 1991) using a jab stick or capture rifle. Following induction, we radiocollared the bears and extracted a premolar tooth to estimate age (Stoneberg and Jonkel 1966). Bears were monitored to ensure their safe recovery, and we did not track them until > 24 hours had passed to allow for resumption of normal activities.

Radiotelemetry

Bears were radio-tracked from the ground during June 1993-December 1995, and we attempted to evenly distribute the locations into three time periods: dawn-1000, 1000-1500, and 1500-dusk. Each bear was located approximately every other day, for an average of three locations per week. Locations were determined using a combination of triangulation (Nams and Boutin 1991), homing (White and Garrott 1990), and direct observation. To triangulate, azimuths were taken from known locations and immediately plotted onto 7.5-minute United States Geological Survey (USGS) orthophoto quadrangle maps. The bear's location was estimated as the center of the error triangle created from the intersection of 3 bearings (Nams and Boutin 1991). The minimum time allowed to get three intersecting bearings was approximately 30 minutes, after which the previous bearings were discarded and the process repeated. Error triangles that encompassed more than one habitat necessitated using the homing method in which the observer walked along the habitat edges contained within the triangle until one habitat was determined to contain the animal. Disturbance was minimized by not directly walking towards the bear and by not approaching bears any closer than necessary to classify the occupied habitat. If, based on bear activity, we believed we may have caused the bear to move, the subsequent location was not used for habitat analyses. Weak or reflected signals due to dense vegetation and rugged topography also at times prohibited classifying a location to habitat. In such cases the triangulation was used only for home range calculation purposes.

Error trials were conducted using 61 locations of test transmitters. Transmitter placement was as unbiased as possible to approximate actual bear tracking, and locations were chosen by a third party to reflect a variety of habitats and topography (Vander Heyden 1997). The trials resulted in a mean linear error of 89 m and a mean areal error triangle of 4 ha. Three of 61 (5%) transmitters were assigned to the wrong stand.

Defining Availability

We determined habitat availability based on the size of female bear home ranges and the area sampled (snared) for bears. We placed a circle with a diameter equal to twice the largest 95%

Minimum Convex Polygon (MCP, Mohr 1947) home range calculated for a female bear (3,595 ha) around every snare site available to capture bears. The area enclosed by the outer boundary of the circles was delineated and used to define the study area perimeter and to determine habitat availability at the landscape scale. Because we wanted to examine habitat use by bears in a managed forest, we excluded areas falling within the Diamond Peak Wilderness from calculations of availability. Use of the largest MCP home range belonging to a resident female bear was intended to delineate a study area large enough to encompass the maximum distances a female bear may have traveled to reach a snare.

Habitat Classification

We created a habitat map from a 1992 LANDSAT Thematic Mapper (TM) image of the study area using Earth Resources Data Analysis System (ERDAS, Atlanta, GA) software for digital-image analysis. The resolution of the TM image was 30 x 30 m (0.09 ha). Thirty spectrally distinct classes were identified, and we used an unsupervised classification (Jenson 1986) to group the classes into six broad habitats with a minimum mapping unit of 4 ha. Field reconnaissance and aerial photograph interpretation were used to further refine the classification. Habitat classes were based on stand structure and approximated a successional hierarchy ranging from early successional grass-forb to mature forest (Table 1). Map accuracy was computed with standard techniques for land cover classification (Lillesand and Kiefer 1979), and described in detail in Vander Heyden (1997). Logging activity between 1992 and the years of this study was minimal, thus we believe that any potential implications of land cover change on map accuracy and habitat analyses were largely inconsequential.

The habitat map was integrated into a GIS along with bear locations, stream, road, and digital elevation model (DEM) coverages. Variables obtained from the DEM included elevation, slope, and aspect. The stream coverage depicted first- through third-order streams, and the road coverage, while it did not distinguish between road types (e.g., primary, secondary), included all roads recognized on USGS orthophotoquads created in 1986. Although an accuracy assessment was not performed on the road layer, we found few discrepancies between it and the actual road system. Secondary, graveled logging roads composed the majority of the roads in the area.

To assess the significance of habitat edges to bears, we constructed an edge buffer with a width of 50 m on either side of every stand boundary. Locations falling within this buffer also were classified into a separate habitat category called "edge." Edge locations were then divided into two

TABLE 1. Habitat classes used by female black bears in the central Cascades of Oregon, 1993-95.

Habitat Class	Description[1]	Proportion in study area
Grass-forb	Very little vertical stand structure; seedling trees and shrubs are not dominant.	0.17
Shrub	Shrubs dominant, trees provide less than 30% crown closure.	0.10
Open-canopy sapling /pole	Canopy closure <60%; shrub understory common.	0.10
Closed-canopy sapling/pole	Canopy closure 60-100%; little ground vegetation.	0.13
Closed-canopy mature timber	Canopy closure >80% but usually <100%; average tree dbh. > 53 cm. Some ground vegetation present.	0.32
Open-canopy mature timber	Canopy closure <80%, average tree dbh. >53 cm. Understory of shrubs, small trees, and other vegetation common.	0.18
Total		1.00

[1]Based primarily on Brown (1985).

TABLE 2. Habitat combinations for the variable "edge type" used in the logistic regression models for female black bears in the central Cascades of Oregon, 1993-95.

Low contrast edge	High contrast edge
Grass-forb/shrub	Grass-forb/open-canopy sapling/pole
Shrub/open-canopy sapling/pole	Grass-forb/closed-canopy sapling/pole
Open-canopy sapling pole/closed-canopy sapling/pole	Grass-forb/closed-canopy mature timber
Closed-canopy/sapling pole/closed-canopy mature timber	Grass-forb/open-canopy mature timber
Closed-canopy mature timber/open-canopy mature timber	Shrub/closed-canopy/sapling/pole
	Shrub/closed-canopy mature timber
	Shrub/open-canopy mature timber
	Open-canopy sapling/pole/closed-canopy mature timber
	Open-canopy sapling/pole/open-canopy mature timber
	Closed-canopy sapling/pole/open-canopy mature timber

categories, "high contrast" and "low contrast" based on the structural contrast of the habitat classes composing the buffer (Table 2).

Home Range Estimates and Analyses

We used two methods to quantify annual home range sizes: the 95% adaptive kernel (ADK) method using the program CALHOME (Baldwin and Kie 1992) with the default parameters, and the 95% minimum convex polygon (MCP) method using the program HOMERANGE (Ackerman et al. 1990). We used the 95% ADK home range in all analyses to facilitate comparisons among bears with variable sample sizes.

Twenty-six annual MCP home ranges were calculated for 14 individuals; 24 ADK home ranges were calculated for 12 individuals. We excluded two bears from the ADK calculations because of small sample sizes (< 24). The number of locations used per bear for the ADK estimates ranged from 24 to 85 with a mean of 48 (SE = 18). In addition, we calculated 95% ADK "composite" (multi-year) home ranges for each bear to determine the overall area used by each bear in the course of the study.

We used analysis of covariance to assess the presence of an association between the following explanatory variables and 95% ADK home range size: individual bear variation defined by the variable "bear", reproductive status, year, and number of locations. We used stepwise backwards variable selection procedures to eliminate insignificant variables ($P \leq 0.05$) from the model.

Habitat Analyses

We investigated habitat selection at two scales, the home range and the landscape, using individuals as the primary sampling units (Thomas and Taylor 1990). For our landscape-scale analysis, we measured habitat use for each radio-marked animal and measured availability over the entire study area; for our home-range-scale analysis, we measured both use and availability at the individual level. Both designs resulted in separate resource selection "functions" for each animal, thereby allowing individuals to vary in their habitat selectivity. We used these individual estimates to make inferences to the population of animals (Cox and Hinkley 1974).

Home Range Scale

Univariate Analysis. —We used a Chi-square goodness-of-fit test (Neu et al. 1974, Byers et al. 1984) to compare habitat availability within the

composite 95% ADK home range for each bear ($n = 12$) to use. This tests the null hypothesis that bears used habitats within their home ranges randomly. We chose $P \leq 0.10$ in recognition of the limited power implicit to our small sample size. When a Chi-square statistic was significant, we constructed Bonferroni 95% confidence intervals (Neu et. al 1974, Byers et. al 1984) to determine which habitat classes differed in use from expected.

Logistic Regression. —We used logistic regression (Ramsey et al. 1994) to identify and model habitat variables that best distinguished known-bear locations (obtained from radio telemetry) from random locations (points). This resulted in odds ratios that described the probability that a particular observation was a bear location. The number of random locations generated within the 95% ADK annual home range for each bear was approximately three times the number of locations obtained from radio telemetry. The ratio of three random points per every known point is optimal in terms of reducing the standard errors of the estimates (Ramsey, pers. comm.).

In addition to habitat class and edge type, we tested the following explanatory variables for significance to bear habitat selection: patch (stand) size, slope gradient, aspect, elevation, and distance to the nearest road, stream, and edge. Slope, aspect, and elevation variables were calculated from a DEM at a scale of 1:250,000 obtained from the USGS. Elevation was measured as a continuous variable; slope and aspect were categorical. Slope was divided into two categories based on gradient. We considered locations falling on slopes ranging from 25-48 degrees "steep" and locations falling on slopes < 25 degrees "moderately steep." Aspect, initially expressed in degrees from 0 to 360, was divided into eight categories, each containing a range of 45 degrees, as well as a ninth category defined as "no aspect." All variables were obtained from digital overlays created within a GIS by use of road, stream, and DEM coverages. These coverages were juxtaposed with the coverage of bear locations, and the GIS was queried for association with known-bear locations and random points.

Initially, we fit a single model for each bear with the largest multiple year sample sizes using "bear" as both a main effect and an interaction term, using a variable selection procedure based on the drop-in-deviance test (Ramsey et al. 1994). This test assesses the contribution of the proposed variables relative to the observed data; variables that led to a significant reduction in model deviance ($P \leq 0.10$) were retained in the model. Interactions were not detected, nor were any variables highly correlated ($r < 0.4$). No year effect was present, which allowed us to combine data from multiple years into one model for each bear (12), using the nine variables described above. These 12 models were then examined, and any variable significantly associated with any bear's habitat selection ($P \leq 0.10$) was included in a "grand" model. Data for each of the 12 bears were then fit to the grand model, using Chi-square and *P*-values from drop-in-deviance tests, which compared the final model with a series of reduced models. This resulted in 12 model summaries each containing the same variables along with their estimated coefficients and standard errors. Lastly, we calculated odds ratios to quantify the effects of each variable, examined if the affects were consistent among bears, and made inferences to the population.

Habitat Analyses: Landscape Scale

Habitat Use By Individual Bears.—We examined habitat use for each bear using a Chi-square goodness-of-fit test ($P \leq 0.10$) to compare habitat availability within the entire study area to use. When the Chi-square statistic was significant for any bear, we constructed Bonferroni 95% confidence intervals to determine which categories differed in use from expected.

Seasonal Habitat Use.—We pooled all bear locations and divided them into three seasons based on plant phenology: spring (den emergence-15 June), summer (16 June-15 September), and fall (September 16-den entry). For each season, we used a Chi-square goodness-of-fit test ($P \leq 0.10$) to determine if observed use of the six habitat classes was different from expected, followed by 95% Bonferroni confidence intervals to determine which habitats were used greater than, equal to, or less than their availability.

Results

Home Range Size

The mean 95% annual ADK home range for 12 bears was 3,212 ha (range: 1,667-8,519 ha, SE =

TABLE 3. Annual and composite (all years) 95% adaptive kernel home range sizes (ADK, ha); annual 95% minimum convex polygon home ranges (MCP, ha), and the number of locations per female black bear radiocollared in the central Cascades of Oregon, 1993-95.

Bear	1993			1994			1995			Composite	
	Size		*n*	Size		*n*	Size		*n*	Size	*n*
	ADK	MCP		ADK	MCP		ADK	MCP		ADK	
93-009[1]		2042.00	19								
93-011	2632.00	2017.00	60	2951.00	1352.00	47	2407.00	2253.00	49	3363.00	156
93-016[2]	3988.00	2359.00	54	2203.00	1639.00	44				4165.00	98
93-018[3]	8519.00	6334.00	30	5845.00	4052.00	34				9149.00	64
93-024[4]	2391.00	8626.00	32								
93-026	2145.00	1348.00	56	1828.00	1220.00	42	5817.00	2143.00	49	2925.00	147
94-037[5]				2168.00	1213.00	35	1954.00	1318.00	85	1835.00	120
94-038[5]				1667.00	1085.00	32	1749.00	1194.00	72	1728.00	104
94-041[5]				2036.00	1033.00	29	2094.00	1411.00	60	2671.00	89
94-045[5]				5939.00	2468.00	25	6315.00	3578.00	80	5238.00	105
94-049[5]				2001.00	9014.00	24	5373.00	2064.00	48	5528.00	72
94-050[5]				1971.00	7650.00	24	2278.00	1290.00	68	2461.00	92
94-051[6]					489.00	21					
95-063[7]							2231.00	1510.00	74		

[1]No Adaptive Kernel Home Range was calculated due to small sample size; bear was killed after 1993.
[2]Mortality, no data after 1994.
[3]Dropped collar, no data after 1994.
[4]Mortality, no data after 1993.
[5]Bears not captured until 1994.
[6]Bear captured in 1994, no data for 1995 because of subsequent mortality.
[7]Bear captured in 1995.

1,716 ha; Table 3). The mean 95% MCP was 2,994 ha (range: 1,033-9,014 ha, SE = 2,189 ha) (Table 3). On average, MCP estimates were 7% smaller than ADK estimates. Composite (multi-year) 95% ADK home ranges averaged 3,906 ha (Table 3).

Adaptive kernel home-range sizes estimates were not significantly related to number of locations ($P = 0.26$), presence of cubs (seven females had cubs of the year, $P = 0.76$), or year ($P = 0.45$). The only variable associated with ADK home range was "bear" ($P = 0.03$).

Habitat Use: Home Range Scale

Univariate Analysis.—Most bears (10 of 12) used habitats disproportionately to their availability within their home ranges. Because low sample sizes limited the power of tests to determine significance, an examination of trends (disregarding significance) is helpful in discerning use patterns among individuals (Table 4). Female black bears used grass-forb less than expected and open-canopy sapling/pole and mature timber classes more than expected. The majority used grass-forb, shrub, and closed-canopy sapling/pole types less than availability, and open-canopy sapling/pole, open-canopy mature timber and closed-canopy mature timber more than availability.

Logistic Regression.—Eight of the nine variables included in the full models for each of the 12 bears were significant for at least one bear; the exception was edge type. The number of significant variables ($P \leq 0.10$) per bear ranged from one to five, including stream distance, aspect, elevation, slope gradient, patch size, road distance, edge distance, and habitat class. These variables explained habitat characteristics that differed between random and known bear locations, and were used to construct a general-habitat-association model (i.e., the "grand" model). The parameter estimates and standard errors are described in detail in Vander Heyden (1997). The results of the grand model are explained below, beginning with the categorical variables.

TABLE 4. Habitat use versus availability within composite home ranges (n=10) of female black bears in the central Cascades of Oregon, 1993-95. Small sample sizes prohibited the ability to find significance at $P \leq 0.10$, therefore a comparison is made at both $P \leq 0.10$ and $P > 0.10$.

	Use compared to expected[1]				
	$P \leq 0.10$			$P > 0.10$	
		Not different			
Habitat Class	Less than	than expected	More than	Less than	More than
Grass-forb	4	5	1	9	1
Shrub	2	7	1	8	2
Open-canopy sapling/pole	0	7	3	3	7
Closed-canopy sapling/pole	2	8	0	7	3
Closed-canopy mature timber	0	8	2	2	8
Open-canopy mature timber	1	6	3	2	8

[1] Selection was based on the Pearson Chi-square goodness-of-fit test and Bonferroni confidence intervals. Expected values were calculated using proportion of habitat classes within 95% adaptive kernel composite home ranges for each bear.

The variable "habitat" was significant for five bears ($P \leq 0.007$). It had six levels (i.e. types of habitat) with grass-forb used as the reference level to which all other habitats were compared. With only one exception (bear 93 - 011), the odds of a location being a known bear location rather than a random point increased from grass-forb to all other habitats. For three of the five bears, open-canopy sapling/pole had the highest odds of a location being known rather than random when compared to grass-forb. The highest odds for the other two bears were for the habitat classes closed-canopy mature timber (bear 93 - 011) and closed-canopy sapling/pole.

"Aspect" was significant for two of the bears in the final models ($P = 0.007$ and $P = 0.002$). These bears were more often found on southeast aspects than at any of the other levels. "Slope gradient", defined by the indicator variable "moderate slope", was significant for two bears at $P = 0.03$, and $P = 0.07$. In both of these models, the odds were higher that a bear location was on a steep slope.

"Stream distance" was significant for four bears, with bear locations tending to be closer to streams than random points. The mean distance to the nearest stream of any order for bears in this study was 167 m (Table 5). "Patch size" was significant for bear 94 - 041 ($P = 0.04$) and bear 94 - 050 ($P = 0.05$). For both of these bears, the odds that a location was a known-bear location became less and less likely as the patch size increased. In other words, these bears were more likely to be found in small patches. "Road distance" was significant for five bears; the odds of a location being known increased the farther from a road the location became. The mean distance to the nearest road in this study was 307 m (Table 5). "Elevation" was significant for three bears; for two of the three, a location was more likely to be a random point (and not a bear location) the higher the elevation became. "Edge distance" was significant ($P = 0.07$) for one bear, 93 - 011. This bear was likely to be found close to habitat edges. The overall mean distance from edge for all bear locations was 62 m (Table 5).

TABLE 5. Mean and standard error (SE) values for known and random continuous variables measured per female black bear (n = 12) in the central Cascades of Oregon, 1993-1995.

	Known		Random	
Variables	$\bar{X}$	SE	$\bar{X}$	SE
Distance to stream (meters)	167.00	97.00	228.00	124.00
Distance to road (meters)	307.00	215.00	287.00	200.00
Distance to edge (meters)	62.00	20.00	64.00	16.00
Patch size (hectares)	682.00	1103.00	693.00	1052.00
Elevation (meters)	968.00	188.00	970.00	240.00

Habitat Use: Landscape Scale

Habitat Use by Individual Bears Compared to Availability in the Study Area.—All but one bear used at least some habitats disproportionately to their availability across the study area landscape ($P \leq 0.10$; Table 6). The habitats used more than availability by any of the bears were open-canopy sapling/pole, and both open-and closed-canopy mature timber. The most frequently under-used

TABLE 6. Number of female black bears (n=11) using each habitat class less than or more than its availability ($P \leq 0.10$) in the central Cascades of Oregon, 1993-95.

	Use compared with expected[1] ($P \leq = 0.10$)		
Habitat Class	Less than	Use not different than expected	More than
Grass-forb	8	3	0
Shrub	4	7	0
Open-canopy sapling/pole	1	3	7
Closed-canopy sapling/pole	2	9	0
Closed-canopy mature timber	1	9	1
Open-canopy mature timber	2	7	2

[1]Selection was based on the Pearson Chi-square goodness-of-fit test and Bonferroni 95% confidence intervals. Expected values were calculated using the proportion of habitat classes within the study area boundary.

habitats were grass-forb (8/11 bears) and shrub (4/11 bears).

Seasonal Habitat Use.—Bonferroni 95% confidence intervals indicated that in the spring, bears used grass-forb less than expected; in the summer, bears used shrubs and closed-canopy mature timber less than expected, and open-canopy sapling/pole and open-canopy mature timber more than expected (Table 7). In the fall, bears used grass-forb and shrub less than expected, and closed-canopy-mature timber more than expected.

Discussion

Black bears are highly opportunistic and extremely mobile; necessary traits in an environment in which food resources vary both temporally and spatially. The patchy and fluctuating nature of black bear food resources leads to diverse selection strategies based on the composition and availability of habitats within each bear's home range. Nonetheless, some consistent trends were evident.

Home Range Size

Home ranges in the Cascades of Oregon were much larger than those reported elsewhere in similar

TABLE 7. Seasonal habitat use[1] by a pooled sample of female black bears (n = 12) in the central Oregon Cascades, 1993 - 1995.

	Season		
Habitat Class	Spring n = 315	Summer n = 448	Fall n = 286
Grass-forb	–	no difference	–
Shrub	no difference	–	–
Open-canopy sapling/pole	no difference	+	no difference
Closed-canopy sapling/pole	no difference	no difference	no difference
Closed-canopy mature timber	no difference	–	+
Open-canopy mature timber	no difference	+	no difference

[1] "–" use less than expected, ($P \leq = 0.10$); "+" use greater than expected, ($P \leq = 0.10$). Selection was based on the Pearson chi-square goodness of fit test and Bonferroni confidence intervals.

habitats. In western Washington, for example, home ranges of black bears were reported to average 4 km^2 (Barber 1983), and 2 km^2 (Lindzey and Meslow 1977) on Long Island, and 5 km^2 (Poelker and Hartwell 1973) in western Washington (mainland). The much larger home range size for female bears in this study may be attributed to lower habitat productivity in the Cascades, or lower densities of bears relative to carrying capacity.

Habitat Use at the Landscape and Home Range Scale

At both the home range and landscape scales, female black bears mostly selected a combination of open-canopy/sapling pole stands, and both open-canopy and closed-canopy mature timber. These stands seemingly offered a combination of light-dependent food plants (berries, in particular) with the security of tree cover. Berries (primarily *Vaccinium* spp.) ripened starting in mid-June, and bears used open-canopy sapling/pole stands more than expected throughout the summer. Both closed and open-canopy mature stands were structurally diverse, had large amounts of downed woody debris, and had a variety of plant species in the understory, especially in canopy gaps. This may explain why closed-canopy mature timber was the most prevalent habitat in 10

of the 12 home ranges, and was used significantly more than expected in the fall, along with open canopy mature timber. These stands presumably offered alternative bear foods as summer foods became scarce, and escape cover when hunting seasons increased vehicular and human disturbance.

In contrast, bears made little use of closed-canopy sapling/pole stands at either scale (Tables 4 and 6). Despite their potential security value, closed-canopy sapling/pole stands may have limited use for black bears in the Central Cascades. Prior to stem exclusion these stands often are extremely dense and little light penetrates the canopy (Brown 1985); understory vegetation, and presumably bear food, is sparse. Grass-forb habitats, although prevalent in many home ranges and often containing bear foods (grass, anthills, berries), were also avoided, with bears more likely to occur in shrub or open-canopy sapling/pole stands. These two seral stages differed from grass-forb primarily in their relative abundance of cover. In agreement with this study, (Lindzey and Meslow 1977) reported that older clearcut units in western Washington were more often selected than recently cut units even when recent cuts apparently had food available. They also found that bears did not begin to use clearcut units greater than availability until the cuts were 18-25 years old. These units approximated our open-canopy sapling/pole habitat, which occurs 10-20 years following clearcutting.

In addition to the potential influence of within-stand cover, adjacency to mature forest may also affect habitat selection. Two of the bears that made use of young seral stages (shrub and open-canopy sapling pole) selected for smaller patches from which forested areas were easily accessible. The home ranges of these two bears were somewhat unique in that they contained large contiguous blocks of forest, with logged stands of early seral condition mainly along the periphery. Activity was concentrated in the smaller of these logged stands; larger stands may have inhibited use because the bears may have been reluctant to forage very far into areas with limited cover. The proximity of cover to feeding areas has been postulated as influencing habitat selection in several other studies (Novick and Stewart 1982, Grenfell and Brody 1986).

The variables related to edge were minimally significant although in both this study and the study in western Washington (Lindzey and Meslow 1977) over half of all bear locations were in edge habitat (< 50 m from the boundary of two habitats). It could be that edge truly did not play a role in habitat selection but rather was an artifact of the high degree of fragmentation in the area. Conversely, perhaps the edge classification, based on structural contrast between habitat types, was inappropriate, or the edge buffer specified, (50 m on each side of a habitat boundary), was too large.

Bears were more likely to occur at increasing distances from the nearest road. Most of the roads in the study area were open to the public, consequently traffic could have caused considerable disturbance to bears especially during the hunting season when traffic levels were high. Additionally, logging activity, although decreased in recent years, may have also contributed to black bears avoidance of roads. Measures of road distances to bear locations vary among studies, and disparate road densities and road types confound comparisons.

In general, bears preferred low elevations, steep slopes, and southeasterly exposures. In corroboration with this study, Novick and Stewart (1982) also found higher activity on drier southern slopes in Southern California, and both Mollohan (1989) and Unsworth et al. (1989) found selection for steep slopes. Exposure influences floristic composition, with southern exposures in our study area containing manzanita, mountain ash, and grass, and slope gradient may confer greater security value and facilitate early detection of threats.

Lastly, bears were more likely to occur close to streams. Young and Beecham (1986) suggested that water may offer important feeding opportunities by influencing the availability of riparian vegetation and perhaps providing fish carcasses and aquatic invertebrates, and Kellyhouse (1980) stated that streamside buffers may provide important cover and travel opportunities in areas otherwise devoid of timber. These observations apply to our study area as well.

Management Implications

Silvicultural techniques that promote the development and maintenance of open-canopy sapling/pole stands and mature timber should benefit black bears. Therefore, decreasing dense canopy closures by thinning, pruning, or creating canopy gaps

would promote the growth of understory vegetation important for both foraging and hiding cover. Maximizing food and cover could likely be achieved by using uneven-age management practices to create structurally diverse stands (Hunter 1990), and maintaining patches containing high plant diversity may provide for a variety of bear foods.

We also suggest minimizing the use of clearcutting, or limiting the size of harvest units. Placing cuts adjacent to mature timber and open-canopy sapling/pole stands would maximize the combination of food and cover and create edge habitat. Lastly, the continued protection of streamside buffers, implementing road closures, and putting old roads "to bed" may encourage use by black bears.

In conclusion, we recommend that black bear management be responsive to vegetation composition and structure, taking into account the effects of roads and streams on habitat selection. Ultimately, what is needed is an understanding of how habitat change affects black bear population viability. To this end, we advocate future research on the effects of forest practices on black bear demography.

Acknowledgements

This paper is a contribution of the Oregon Cooperative Wildlife Research Unit at Oregon State University, the U.S. Fish and Wildlife Service, U.S. Geological Survey Biological Resource Division, and was produced with the cooperation of the Wildlife Management Institute. The Oregon Department of Fish and Wildlife supported this research, and provided logistic, technical, and field assistance. T. O'Neil was instrumental to the success of this project, and K. Laudon provided invaluable field assistance. T. Maan provided statistical services; M. Wing and G. White conducted numerous GIS - related tasks and spatial analyses, and C. Kiilsgaard oversaw the production of the LANDSAT classification. We thank F. T. van Manen, F. G. Lindzey, and J. Ratti for review of the manuscript and helpful comments.

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Received 31 January 1999
Accepted 18 August 1999

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Wolverine Distribution in the Northwestern United States and a Survey in the Seven Devils Mountains of Idaho

Abstract

The distribution and connectivity of wolverine (*Gulo gulo*) populations in the northwestern United States is largely unknown. We investigated the potential distribution of wolverine in the Northwest and the importance of the Seven Devils Mountains for connecting populations in Idaho and Oregon. Mapping documented sightings suggested 3 relatively distinct subpopulations in the 1) Cascade Mountains of Washington, 2) Cascade Mountains of Oregon, and 3) Rocky Mountains of Idaho. Sightings across mountainous habitats of Oregon also suggest that the Seven Devils Mountains may provide the only suitable habitat linking wolverine subpopulations in Idaho and Oregon. We confirmed the first observation of a wolverine in the Seven Devils Mountains during a helicopter survey in March 1998. The lack of previous sightings suggested limited dispersal between Oregon and Idaho. Low dispersal may impact the regional viability of wolverine by lowering the likelihood that suitable habitat patches are inhabited over time. Maintaining and enhancing the integrity of movement corridors between the Seven Devils Mountains and other contiguous mountain habitats in Idaho and Oregon may be essential for ensuring regional wolverine persistence.

Introduction

Wolverine (*Gulo gulo*) populations are suspected to be small, especially sensitive to environmental perturbations, and vulnerable to local extinction (Banci 1994). This has resulted in administrative protection with the wolverine classified as a Species of Concern by the U.S. Fish and Wildlife Service and many western states, and Sensitive Species by the U.S. Bureau of Land Management and U.S. Forest Service (Conservation Data Center 1994, Oregon Natural Heritage Program 1998). An ecological understanding of a sensitive species range is essential for developing conservation strategies (Ruggiero et al. 1994). Few wolverine surveys have been conducted, however, leaving the distribution and connectivity of populations in the western United States largely unknown.

The Seven Devils Mountains are believed to contain suitable wolverine habitat and may provide an important corridor linking known populations in central Idaho (Copeland 1996) and northeast Oregon (Schommer 1994). However, the lack of wolverine surveys in the Seven Devils Mountains leaves the presence of this sensitive species unconfirmed. To understand the importance of the Seven Devils Mountains for conserving wolverine populations in the northwestern United States, our objectives were to 1) construct a hypothesized distribution map for wolverine from existing data, 2) identify potential movement corridors in the region, and 3) confirm the presence of wolverine in the Seven Devils Mountains.

Study Area

The Seven Devils Mountains are in west-central Idaho and bordered by the Little Salmon River to the east and Snake River to the west. Elevations range between approximately 365 m on the Snake River and 3035 m at the tallest peak. Most of the mountain range is in the Hells Canyon Wilderness Area and Hells Canyon National Recreation Area, which is administered by the U.S. Forest Service, Wallowa-Whitman National Forest.

The Seven Devils Mountains are composed of jagged peaks with montane, sub-alpine, and alpine habitats (U.S. Department of Agriculture 1990). At least 2 episodes of island-arc volcanism and adjacent marine sedimentation formed the Seven Devils Mountains over 20,000 years ago. Glaciation created numerous high-elevation cirque basins of which many contain lakes.

Vegetation patterns in the Seven Devils Mountains follow gradients associated with elevation,

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topography, and precipitation (U.S. Department of Energy 1985, Harker et al. 1993). Bunchgrass, coniferous woodlands, and subalpine forest communities dominate lower, mid, and high elevations, respectively (Daubenmire 1970, Johnson and Simon 1987). Cirque basins, however, have sparse overstory cover because large rock talus limits tree establishment.

Methods

To determine the potential distribution of wolverine in the Northwest, records of wolverine sightings were requested from the 1) Washington Wildlife Heritage Database, 2) Oregon Natural Heritage Program, and 3) Idaho Conservation Data Center. Sightings were plotted to develop a hypothesized species distribution map for the region. All data were plotted regardless of observer reliability, because most unconfirmed sightings were spatially correlated with confirmed sightings at the regional resolution, and no standard criteria for screening sightings have been developed (Maj and Garton 1994).

We defined the Seven Devils survey area to include all land cover ≥2123-m (≥7000-feet) elevation (Copeland 1996) within a boundary formed by the: 1) Snake River on the west, 2) Little Salmon River on the east, 3) extent of the Hells Canyon Wilderness Area on the north, and 4) Crooked River on the south. Standard ground-based survey methods, such as photographic bait stations (Zielinski and Kucera 1994), are not applicable for the remote setting of the Seven Devils Mountains. Copeland (1996) suggested that aerial surveys during February and March might provide a reliable method for detecting wolverine presence. In Idaho, wolverines predictably placed reproductive dens on north- to east-facing talus slopes of isolated, high-elevation cirques with low tree cover. Snow trails created during movements to and from den sites were highly visible from aircraft.

To focus our aerial-survey effort where detection probabilities were relatively high, we applied the GIS-based wolverine habitat model of Hart et al. (1996) to the survey area. The GIS-based model predicted habitat suitability within 30-m pixels superimposed over the landscape using spatial, vegetational, and physiographic characteristics described by Copeland (1996). We then subdivided the survey area into 64 search units that captured the spatial arrangement of predicted suitable habitat. Boundaries were defined using easily identified watershed features to facilitate a contour-following helicopter survey (Unsworth et al. 1994). Clusters of search units with concentrations of predicted suitable habitat were selected for surveying.

A single helicopter survey was conducted 19 March 1998. Flight paths followed approximately 150-m elevation contours that completely covered the search unit. When possible, we landed for close inspection of potential wolverine tracks. Otherwise we hovered within 2 m of the snow surface. Survey conditions were optimal for snow-tracking with fresh snow, clear skies, and light winds.

Results

A query of the three wolverine databases revealed 587 (287 in Idaho, 150 in Oregon, and 150 in Washington) documented sightings in the Northwest. Sightings have increased steadily since the 1960s with proportional contributions from each state remaining relatively constant (Figure 1). We believe that increased reporting effort and greater human access to remote habitats accounted for most of the increase in sightings over time (Maj and Garton 1994).

Plotting these sightings on a large-scale topographic map indicated mountainous habitat was the only obvious landscape characteristic associated with our hypothesized distribution of wolverine at the regional level (Figure 2). Most sightings in Idaho occurred in the central portion of the state which contains large tracts of mountainous habitat associated with the northern Rocky Mountains and supports a reproducing wolverine population (Copeland 1996). Similarly, most sightings in Oregon were associated with the Cascade and Wallowa mountains in the west-central and northeastern portions of state, respectively. In Washington, most sightings spanned from the northern Cascade Mountains to the northeastern portion of the state (Figure 2).

The Seven Devils survey area was 20,282 ha with 2161 ha (11%) predicted to be suitable habitat. During 3.5 hours of flying, we surveyed 23 (36%) of the 64 search units, which comprised 7139 ha (35%) of the total survey area and 1033 ha (48%) of predicted suitable habitat. We located and confirmed with ground inspection one set of wolverine

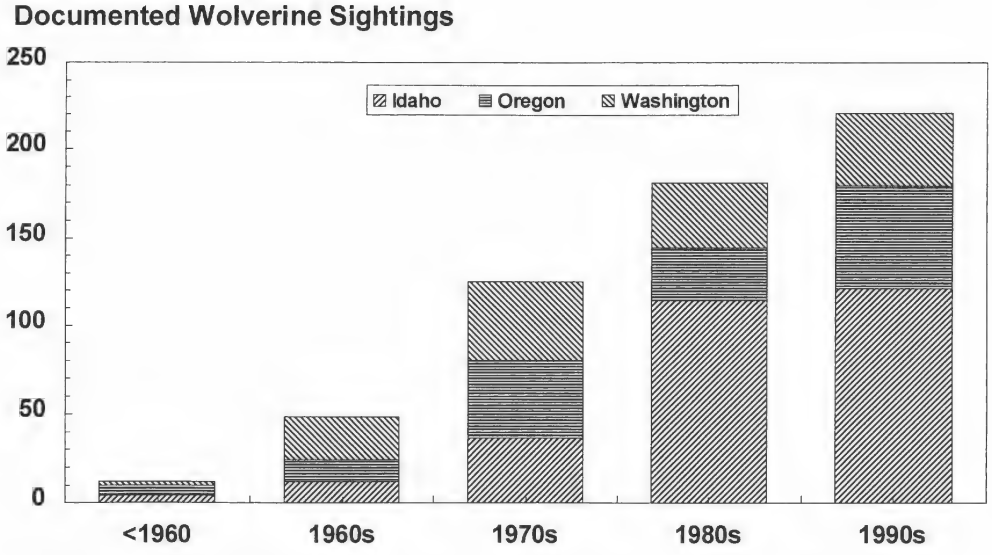


Figure 1. Temporal distribution of wolverine sightings documented in the northwestern United States, 1896-1998.

tracks (Halfpenny et al. 1995). We followed the tracks in both directions until they were obscured by forested canopy. No den or other indication of reproductive activity was detected.

Our observation was the first of a living wolverine in our survey area. Only a dead wolverine, found in 1987 near the Rapid River, had been previously documented. Adjacent to our survey area, the most recent (<3 years) and nearest (<30 air-km) sightings in northeast Oregon and central Idaho were January 1998 in the Wallowa Mountains and September 1995 near McCall, Idaho, respectively.

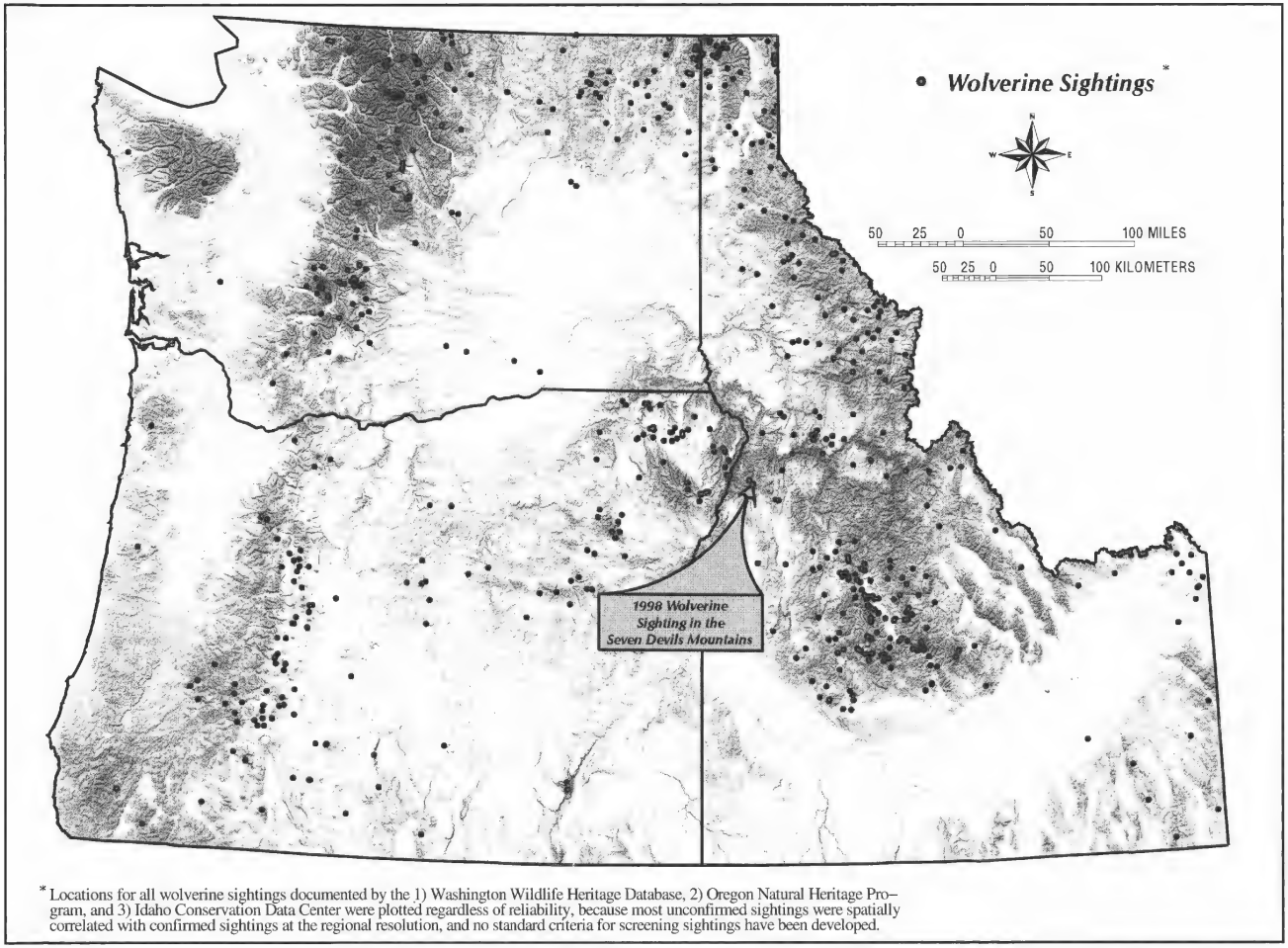
Discussion

Simple visual inspection of wolverine sightings plotted at the regional scale suggested three somewhat distinct clusters within our hypothesized distribution of wolverine (Figure 2). These clusters corresponded to the 1) northern Cascade Mountains in Washington, 2) southern Cascade Mountains in Oregon, and 3) northern Rocky Mountains in Idaho. The clusters may represent three subpopulations within a larger, spatially-structured population in the northwestern United States.

The Columbia River Gorge is a compelling barrier for separating subpopulations in the northern and southern Cascades. Shrub-steppe habitats of the Columbia Plateau and northern Great Basin likely separate the northern Rocky Mountain subpopulation from the northern and southern Cascade subpopulations (Banci 1994). All three subpopulations described here are likely peninsular extensions of a more extensive Canadian population (Banci 1994, Verts and Carraway 1998:427).

Although relatively discrete, the linear east-west scatterings of sightings across Washington and Oregon suggest that individuals inhabiting and moving along corridors of mountainous habitats may connect the three subpopulations to some degree (Figure 2). Therefore, wolverine demographics in these three areas may be correlated through the exchange of individuals among spatially separated subpopulations supporting the potential for metapopulation dynamics (Hanski and Gilpin 1991, Wells and Richmond 1995).

Individual wolverines are capable of making long-distance movements over relatively short periods and may move among subpopulations through the mountainous habitats of northern Idaho, northern Washington, and central Oregon (Figure 2). The scattering of sightings across the arid mountains of central Oregon suggest a movement corridor from the Cascade Mountains to the Wallowa Mountains. Adjacent to this potential


Wolverine Sightings *
50 25 0 50 100 MILES
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1998 Wolverine Sighting in the Seven Devils Mountains
* Locations for all wolverine sightings documented by the 1) Washington Wildlife Heritage Database, 2) Oregon Natural Heritage Program, and 3) Idaho Conservation Data Center were plotted regardless of reliability, because most unconfirmed sightings were spatially correlated with confirmed sightings at the regional resolution, and no standard criteria for screening sightings have been developed.

Figure 2. Distribution of wolverine sightings documented in the northwestern United States, 1896-1998.

movement corridor, the Seven Devils Mountains form a bottleneck of mountainous habitats between Oregon and Idaho. Hence, the Seven Devils Mountains may provide the only suitable habitat linking the reproducing population in central Idaho (Copeland 1996) with northeast Oregon, and also potentially with the southern Cascade Mountains.

Although we confirmed the presence of wolverine in the Seven Devils Mountains, the lack of previous sightings may indicate a small resident population with low interchange rates, raising questions about landscape barriers limiting movement to and from the Seven Devil Mountains (Stamps et al. 1987). The deep gorges of Hells Canyon and the Salmon River Canyon surrounding the Seven Devils Mountains may function as a geographic barrier to population movement. Dominated by low-elevation steppe habitats, these two canyons dissect the Seven Devils Mountains from northeast Oregon and central Idaho.

Wolverines dispersing from "source habitats" (as defined by Pulliam and Danielson 1991) in central Idaho, may be reluctant to cross canyon habitats. Assuming that these canyon habitats are relatively unsuitable (Banci 1994), the Seven Devils Mountains may resemble a stepping-stone connection (Noss 1991) and explain the lack of wolverine sightings in apparently suitable habitat. Movement rates in corridors composed of stepping-stones may be lower than in continuous-habitat corridors (Anderson and Danielson 1997). Additionally, species with inherently low densities often exhibit low dispersal rates and limited population interspersion. Dispersal carries an increased risk of mortality which may be additive in low-density species such as the wolverine. Consequently, limited dispersal may impact long-term regional population viability by reducing subpopulation connectivity and lowering the likelihood that suitable habitat patches are colonized and recolonized over time (Fahrig and Paloheimo 1988, Hansson 1991).

Generating a hypothesized distribution map and confirming wolverine presence is a first step toward identifying the spatial structure of subpopulations and key movement corridors responsible for maintaining this structure in the Northwest. However, additional understanding of 1) reproducing subpopulations, 2) source-sink habitat patches, 3) movement corridors, and 4) movement patterns within and among spatially-structured subpopulations is necessary for monitoring regional population status (Fahrig and Merriam 1985, Harrison 1991). Movement patterns among Idaho, Oregon, and Washington must be identified to specifically understand the potential importance of the Seven Devils Mountains for conserving wolverine and informed regional conservation planning in the Northwest (Banci 1994, Fahrig and Merriam 1994).

Acknowledgments

We thank Melissa Hart and the University of Montana's Spatial Analysis Lab for GIS analyses. We also thank Mike Butler and Idaho Power Company for extensive GIS and mapping support. Mike Wisdom provided analytical insight, and Toni Holthuijzen assisted with earlier drafts of this manuscript. This study was cooperatively funded (CCS 6-16-97-392) by the Wallowa-Whitman National Forest, Idaho Department of Fish and Game, Oregon Department of Fish and Wildlife, and Idaho Power Company.

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Received 27 April 1999
Accepted 13 September 1999

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The Relationship of Douglas-fir Dwarf Mistletoe (*Arceuthobium douglasii*) to Stand Conditions and Plant Associations in the Southern Cascade Mountains, Oregon

Abstract

Douglas-fir dwarf mistletoe (*Arceuthobium douglasii*) is a parasitic plant widely distributed on Douglas-fir (*Pseudotsuga menziesii*) in southwestern Oregon. This study examined the relationship of frequency of occurrence and severity of Douglas-fir dwarf mistletoe with stand conditions and plant associations in the southern Cascade Mountains in Oregon. Data were collected from a subsample of existing permanent plots. Fifteen stand variables and the level of dwarf mistletoe infection in all live Douglas-fir were measured at each plot. Douglas-fir dwarf mistletoe occurred most frequently in the white fir (*Abies concolor*) series. It occurred least in the Douglas-fir series. It occurred in plots at significantly higher elevations, with lower mean annual temperatures and lower mean annual and dry season precipitation than plots where it was absent. Occurrence of Douglas-fir dwarf mistletoe was also significantly associated with steeper slopes, andesite and basalt soil parent materials, lower basal area, and lower percentage of Douglas-fir in the stand. The average plot Dwarf Mistletoe Rating did not differ significantly among climax series. Average plot Dwarf Mistletoe Rating did increase significantly as total basal area decreased and age of the oldest canopy layer increased. Our study suggests that climax series could be used as indicators of the relative frequency of Douglas-fir dwarf mistletoe in the southern Cascade Mountains in Oregon.

Introduction

Douglas-fir dwarf mistletoe (*Arceuthobium douglasii* Engelmann) is a parasitic plant found almost exclusively on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). It causes one of the most widespread diseases of Douglas-fir in the forests of southwestern Oregon (Hadfield 1985) and the interior West (Hawksworth and Wiens 1996). Severe infections cause significant losses in Douglas-fir growth, increased tree mortality, and increased fire hazard (Hawksworth and Wiens 1996). The weight of the brooms caused by Douglas-fir dwarf mistletoe infection can predispose branches to breaking, posing serious hazards in developed recreation sites (Hadfield 1999). However, the brooms caused by Douglas-fir dwarf mistletoe infection are an important component of the habitat of several birds and mammals including northern spotted owls (*Strix occidentalis* var *caurina* Xantus de Vesey), northern goshawks (*Accipiter gentilis* Linnaeus) and many of their prey species (Parks et al. 1999).

All aspects of forest management including recovery plans for the northern spotted owl, habitat management for other sensitive species, watershed restoration programs and timber production require accurate prediction of stand development to prescribe activities that will achieve desired future conditions. Stand development is affected by the frequency and severity of diseases such as Douglas-fir dwarf mistletoe. Information on the relationships between dwarf mistletoe frequency and severity, and forest conditions could be used to guide management plans at both stand and landscape levels. For example, silvicultural methods employed to encourage rapid tree growth that also favor mistletoe spread may be poor choices where the frequency of mistletoe is high. However, some areas where Douglas-fir dwarf mistletoe is frequent and severe may be best used to manage wildlife species that use the large brooms formed in severely infected trees (Parks et al. 1999).

Information about relationships that may exist between plant associations and the frequency of occurrence and severity of Douglas-fir dwarf mistletoe is useful because land stratification based on vegetation potential is a system that is widely used, can be mapped, and incorporates much of the information about site conditions. Areas with the same plant association can be expected to show the same general successional response

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to disturbance, including disturbance caused by pathogenic organisms such as dwarf mistletoes (Layser 1974, Cooper et al. 1991).

Previous studies have shown that there are relationships between the occurrence and severity of dwarf mistletoes, and stand conditions. Hawksworth (1959, 1968), Larson et al. (1970), Acciavatti and Weiss (1974), and Gottfried and Embry (1977) found that the occurrence and severity of several dwarf mistletoe species were associated with aspect, slope, elevation, site and topographic factors. Smith (1972), Hanks et al. (1983), Mathiasen and Blake (1984), and Merrill and Hawksworth (1987) found that the occurrence and severity of dwarf mistletoes differed by habitat type. However, the specific relationships found in these studies varied widely. The variations may have been due to differences in study designs, but it also suggests that these relationships vary according to local conditions and probably differ among geographical areas, hosts, and dwarf mistletoe species. Our study examined the relationship among stand conditions, plant associations, and the occurrence and severity of Douglas-fir dwarf mistletoe in the southern Cascade Mountains in Oregon (Marshall 1995).

Methods

Study Area and Data Collected

The study area was in the southern Cascade Mountains west of the Cascade crest on the Rogue River and Umpqua National Forests in Oregon (Figure 1). We used an existing network of permanent plots established by USDA Forest Service ecologists to identify the plant associations (Atzet and McCrimmon 1990). The locations of these permanent plots were selected by driving along roads throughout the two Forests and sampling mature, relatively undisturbed stands adjacent to the roads. The plot center was determined by walking into the stand the distance necessary to eliminate edge effect from the road, usually 15 to 60 meters. Presence or absence of disease was not a factor in stand selection and was unknown until the plot center was established (T. Atzet, USDA Forest Service, 1999, personal communication).

In 1992, we collected data from a random subsample of the permanent plots to determine the variability in the occurrence and level of Douglas-fir dwarf mistletoe infection (severity) among individual plant associations in the study area. The variability in occurrence and severity was so great that not enough existing plots were available in most of the plant associations for a statistically valid sample. Therefore, the plant associations were grouped according to their climax series: the *Abies concolor* (white fir) series, the *Pseudotsuga menziesii* (Douglas-fir) series, and the *Tsuga heterophylla* (western hemlock) series. These three series cover 75 percent of the study area and have a high constancy of Douglas-fir (Atzet and McCrimmon 1990).

Our preliminary data also showed that, on average, where infection was present, at least one mistletoe-infected Douglas-fir was tallied by the time nine live Douglas-fir closest to the plot center were tallied. Eighty-six percent of the time, the most severely infected Douglas-fir tree in the area was tallied by the time fifteen live Douglas-fir closest to the plot center were tallied. Based on this information, fifteen live Douglas-fir per plot were judged adequate to assess both the occurrence and severity of Douglas-fir dwarf mistletoe in these three climax series.

In 1993, we sampled a total of 168 plots in the three climax series: 40 plots in the Douglas-fir series, 85 plots in the white fir series and 43 plots in the western hemlock series. A sample plot was placed at each selected permanent plot. Sample plots were circular, varied in size, and were just large enough to include the nearest fifteen live Douglas-fir at least 12.7 cm dbh (diameter at breast height, 1.5 meters above ground level). The level of Douglas-fir dwarf mistletoe in each Douglas-fir tree was determined using the Hawksworth six-class dwarf mistletoe rating (DMR) system (Hawksworth 1977). The climax series, elevation (m), mean annual temperature (°C), mean annual precipitation (cm), dry season precipitation (cm, May through September), and soil parent material (andesite, basalt, granite, pyroclastic, sedimentary) of each plot were derived from data from Atzet and McCrimmon (1990). We measured ten additional variables from each plot center: 1) site index (average height (m) at 100 years of three to five dominant, uninfected Douglas-fir in or near the plot using site class tables prepared by McArdle et al. 1961), 2) aspect (north, east, south, west), 3) slope (percent), 4) topographic position (lower, middle, upper), 5) topographic shape (convex, concave, flat), 6) total stand

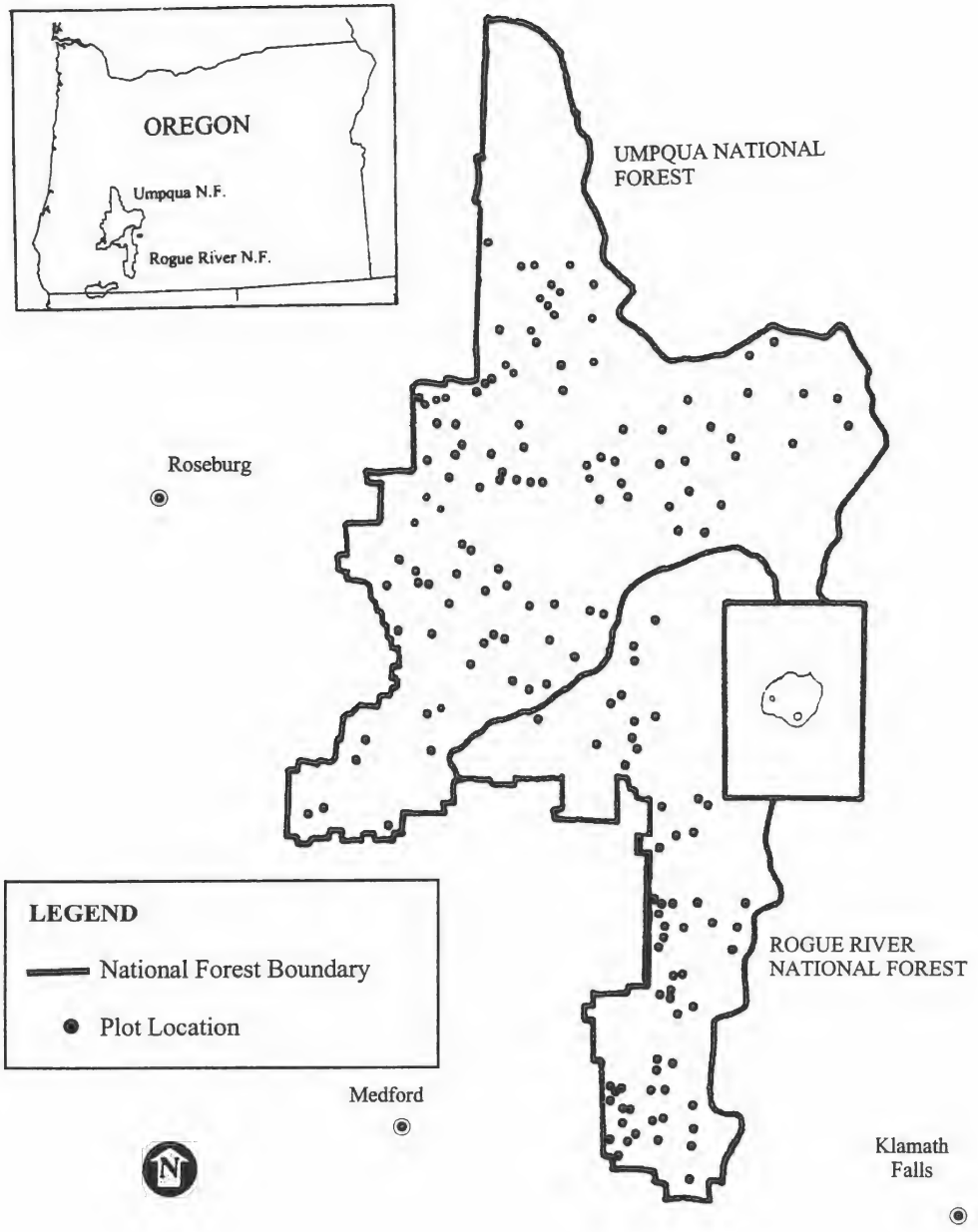

Figure 1. Location of study plots in the southern Cascade Mountains, Oregon.

basal area (cross-sectional area of tree boles at 1.5 meters above ground level, m^2/ha), 7) Douglas-fir stand basal area (m^2/ha), 8) Douglas-fir dbh (cm), 9) number of tree canopy layers, and 10) the age of each canopy layer (years). The percentage of Douglas-fir in each plot was calculated by dividing Douglas-fir stand basal area by total stand basal area.

Statistical Analysis

Analysis of the data was on a per plot basis, due to the variable size of the plots. Infected plots were those containing one or more infected Douglas-fir. The frequency of occurrence of Douglas-fir dwarf mistletoe was defined as the percentage of infected plots. T-tests (Ramsey and Schafer 1997) were used to test for significant differences ($P \leq 0.05$) in the means of the continuous variables between plots with and without infected Douglas-fir. Chi-square (Ramsey and Schafer 1997) was used to test for significant differences ($P \leq 0.05$) in the percentage of plots with infected Douglas-fir among the climax series and other categorical variables.

The average plot dwarf mistletoe rating (mean DMR), or severity of Douglas-fir dwarf mistletoe in each plot, was calculated from the sum of individual DMR of each live Douglas-fir (including uninfected Douglas-fir) divided by the number of live Douglas-fir. The ratio of highest to lowest mean DMR was greater than ten, causing this data to be non-linear. A LOG (base 10) transformation was used to make the mean DMR data linear (Stafford and Sabin 1994). Only infected plots (mean DMR>0) were used to analyze severity. During data collection we discovered that some plots had been disturbed in the past, particularly by harvest of scattered individual trees. Since disturbance is known to affect the severity of dwarf mistletoes (Parmeter 1978), those plots were also omitted, leaving 20 uncut, infected plots for this analysis. Stepwise multiple regression (Ramsey and Schafer 1997) was used to analyze the relationship between LOG(mean DMR) and the continuous variables and then to derive an equation that would best explain the variation in LOG(mean DMR). One-way analysis of variance (ANOVA) was used to test equality of LOG(mean DMR) among the climax series and other categorical variables. Relationships were considered significant with P-values≤ 0.05.

Results

The white fir series is the most widespread in the study area. In general, it is cooler and wetter than the Douglas-fir series and cooler and drier than the western hemlock series. Only the western hemlock series is more productive. The western hemlock series is most widespread on the Umpqua National Forest portion of the study area, but is also common in the northern part of the Rogue River National Forest. It has more precipitation (both mean annual and summer) than the other two series and is intermediate in temperature. This series has the highest productivity of all series in the Cascade Mountains. The Douglas-fir series occurs in the hottest, driest forest environments in southwest Oregon (Atzet and McCrimmon 1990). It is generally the hottest and driest of the three series in the study, although some Douglas-fir series plots in the northern part of the study area were wetter than white fir plots further south. Series characteristics are summarized in Tables 1 and 2.

Dwarf Mistletoe Frequency

Thirty-eight percent of the plots in the white fir series contained Douglas-fir dwarf mistletoe-infected trees, compared to 19 percent in the western hemlock series and three percent in the Douglas-fir series. Actually, infection occurred in only one plot in the Douglas-fir series (Table 3). Chi-square comparison showed significantly more Douglas-fir dwarf mistletoe in the white fir series than in the Douglas-fir series ($P<0.001$). However, the contribution of mistletoe frequency in the western hemlock series to the comparison was not significantly different from that of the other two series. The six warmest plant associations had no Douglas-fir dwarf mistletoe (Figure 2). Three of these associations were in the Douglas-fir series, two were in the western hemlock series and one was in the white fir series. They were the warmest associations in each of their respective climax series. All were moderately wet associations.

Plots with infected Douglas-fir were at significantly higher elevations than plots with no infected Douglas-fir in the white fir and western hemlock series (Table 4). All of the plots with infected Douglas-fir were above 1000 meters in elevation.

TABLE 1. Mean values and standard deviations of continuous variables by climax series in the study area

Series		Elev (m)	Matemp[1] (°C)	Maprecip[2] (cm)	Dsprecip[3] (cm)	Site Index (m/100yr)	Slope (%)	Total BA (m^2/ha)	DFBA[4] (m^2/ha)	% DF[5] (%)	Canopy Layers (no.)	Canopy Age (yr)	Mean dbh[6] (cm)
Douglas-fir	Mean	848.8	9.0	134.3	18.3	34.3	43.7	73.4	63.5	85.9	2.5	195.9	42.2
	SD	211.7	1.1	28.4	2.4	6.4	18.9	17.6	19.3	15.4	0.6	88.3	13.7
white fir	Mean	1215.7	7.1	136.7	18.4	36.9	27.7	74.4	46.3	60.9	2.6	238.4	63.7
	SD	214.1	1.0	25.6	2.9	7.1	18.6	16.8	25.5	27.9	0.5	105.0	25.2
western hemlock	Mean	1014.2	8.0	156.5	20.6	37.1	36.5	77.2	49.8	63.1	2.9	338.7	76.5
	SD	277.7	1.4	19.4	2.6	8.4	21.9	15.3	21.0	20.2	0.3	129.0	19.8

[1]Matemp = mean annual temperature
[2]Maprecip = mean annual precipitation
[3]Dsprecip = dry season precipitation (May through September)
[4]DF BA = basal area that is Douglas-fir
[5]% DF = percent Douglas-fir
[6]dbh = diameter breast height

TABLE 2. Number of plots in each level of categorical variables by climax series in the study area

Series	Soil parent material[1]					Aspect				Topographic position			Topographic shape		
	and	bas	gran	pyro	sed	north	east	south	west	lower	middle	upper	concave	convex	flat
Douglas-fir	10	7	3	20	0	1	5	22	12	5	15	20	12	26	2
white fir	35	31	8	10	1	17	19	27	22	17	30	38	47	32	6
western hemlock	12	15	3	12	1	10	10	9	14	19	5	19	20	22	1

[1]Soil parent material: and = andesite, bas = basalt, gran = granitic, pyro = pyroclastic, sed = sedimentary

TABLE 3. Occurrence of Douglas-fir dwarf mistletoe in plots by climax series in the study area

Series	Number of plots	Number of plots infected
Douglas-fir	40	1
white fir	85	32
western hemlock	43	8
All plots	168	41

Within the white fir and western hemlock series, plots with infected Douglas-fir had significantly lower mean annual temperatures than plots without infected Douglas-fir (Table 4). All of the plots with infected Douglas-fir had mean annual temperatures between 6° and 8°C (Figure 2). No Douglas-fir dwarf mistletoe was found in plots with mean annual temperatures greater than 8°C.

Within the white fir series, plots with infected Douglas-fir had significantly lower mean annual and dry season precipitation levels than plots without infected trees (Table 4), although some plots with infected trees were found at all but the highest levels of both mean annual and dry season precipitation. Plots with infected Douglas-fir had mean annual precipitation levels of 76 to 190 cm, and mean dry season precipitation levels of 15 to 25 cm. There were no significant differences in mean annual or mean dry season precipitation levels among plots in the western hemlock series. Since only one plot in the Douglas-fir series was infested, plots within this series could not be compared statistically. However, the plot that did have infected Douglas-fir occurred on a relatively high elevation, cool, dry site at 1066 m elevation, with 8°C mean annual temperature and 76 cm mean annual precipitation (Figure 2).

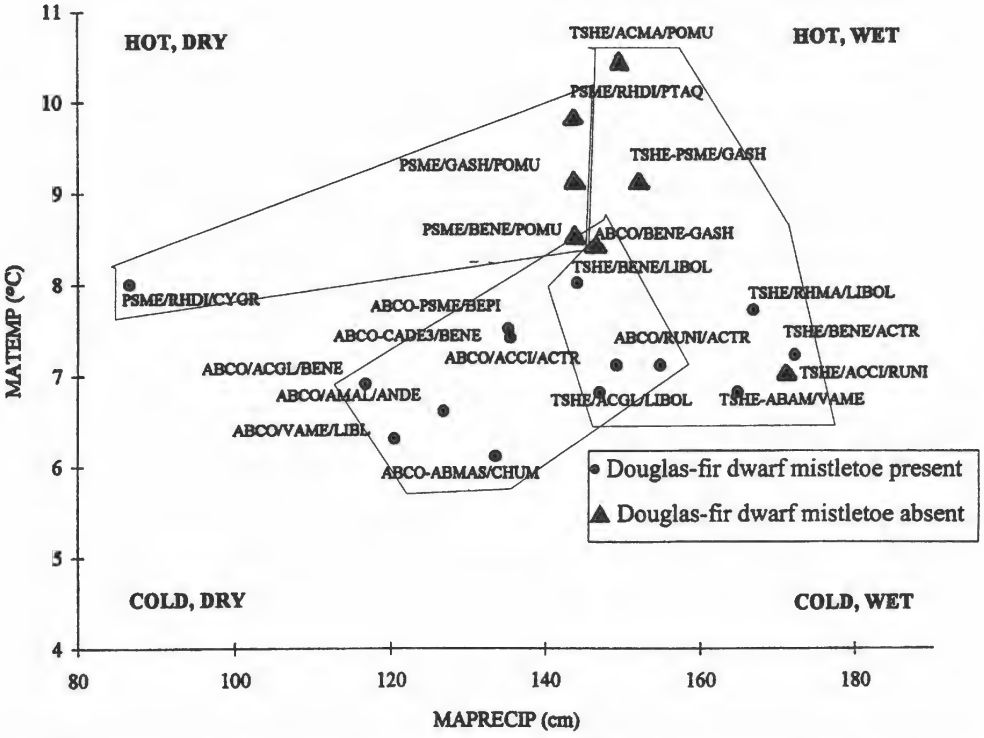

Figure 2. Ecograph of plant associations[1] by mean annual temperature and mean annual precipitation of the sampled plots in southern Oregon.

[1]ABAM = *Abies amabilis*, ABCO = *Abies concolor*, ABMAS = *Abies magnifica shastensis*, ACCI = *Acer circinatum*, ACGL = *Acer glabrum*, ACMA = *Acer macrophyllum*, ACTR = *Achlys triphylla*, AMAL = *Amelanchier alnifolia*, ANDE = *Anemone deltoidea*, BENE = *Berberis nervosa*, BEPI = *Berberis piperiana*, CADE3 = *Calocedrus decurrens*, CHUM = *Chimaphila umbellata*, CYGR = *Cynoglossum grande*, GASH = *Gaultheria shallon*, LIBOL = *Linnaea borealis longifolia*, POMU = *Polystichum munitum*, PSME = *Pseudotsuga menziesii*, PTAQ = *Pteridium aquilinum*, RHDI = *Rhus diversiloba*, RHMA = *Rhododendron macrophyllum*, RUNI = *Rubus nivalis*, TSHE = *Tsuga heterophylla*, VAME = *Vaccinium membranaceum*.

Occurrence of Douglas-fir dwarf mistletoe was also significantly associated with slope, Douglas-fir basal area, and the percentage of Douglas-fir (Table 4). Plots with infected Douglas-fir had both significantly less Douglas-fir basal area and a smaller percentage of the total basal area in Douglas-fir than plots without infected Douglas-fir. The average slope of plots with infected Douglas-fir was significantly less than the average slope of plots without infected Douglas-fir. However, plots with infected trees were found on all but the steepest slopes.

Douglas-fir dwarf mistletoe occurred in a significantly smaller percentage of plots with soil derived from pyroclastic or sedimentary parent materials than in plots with other types of soil parent materials (Table 5). Basalt and andesite parent materials had the highest percentages of plots with infected Douglas-fir.

There were no significant associations between the occurrence of Douglas-fir dwarf mistletoe and aspect, topographic shape, topographic position (Table 5), or site index, total basal area, the number of canopy layers, the age of the oldest canopy layer, and the mean dbh of Douglas-fir (Table 4).

Dwarf Mistletoe Severity

There was no significant difference in mean DMR between the white fir and western hemlock climax series (P=0.86). The Douglas-fir series could

TABLE 4. Mean values of continuous variables between plots with and without Douglas-fir dwarf mistletoe in the study area

Variable[1]	Mistletoe Occurrence	Mean	SE	*P*
Elev	No	1000.1	23.8	
	Yes	1314.2	18.8	>0.01
Matemp	No	8.2	0.1	
	Yes	6.6	0.1	>0.01
Maprecip	No	145.4	2.2	
	Yes	128.2	4.1	0.0002
Dsprecip	No	19.3	0.3	
	Yes	18.0	0.5	0.009
Site Index	No	36.3	0.6	
	Yes	36.4	1.1	0.91
Slope	No	35.8	1.8	
	Yes	27.3	3.1	0.02
Total BA	No	75.5	1.4	
	Yes	73.1	2.8	0.42
DF BA	No	54.5	2.0	
	Yes	41.6	4.2	0.003
% DF	No	71.6	2.1	
	Yes	54.3	4.3	0.0001
Canopy layers	No	2.7	0.1	
	Yes	2.8	0.1	0.15
Canopy age	No	256.6	10.8	
	Yes	245.6	17.6	0.61
Mean dbh	No	60.4	2.2	
	Yes	66.5	3.8	0.17

[1]For description of variables and units of measure, see Table 1.

TABLE 5. Occurrence of Douglas-fir dwarf mistletoe by level of four categorical variables in plots in the study area

Variable	Level	Number of of plots	Number of plots infected	*P*
Aspect	north	27	11	
	east	35	8	
	south	57	10	
	west	49	12	0.14
Topographic position	lower	41	6	
	middle	50	16	
	upper	77	19	0.16
Topographic shape	concave	79	23	
	convex	80	16	
	flat	9	2	0.40
Soil parent material	andesite	57	19	
	pyroclastic	42	2	
	basalt	53	18	
	granitic	14	2	
	sedimentary	2	0	0.004

not be included in the comparison because the only infected plot in the series had evidence of past cutting. There were no significant relationships between mean DMR and any of the categorical variables ($P \geq 0.17$).

Stepwise multiple regression showed that the following equation best explained the variation in severity in uncut, infected plots (P-to-enter≤ 0.05):

LOG(mean DMR) = -2.086 + 0.006(ELV) - 0.034(MAP) - 0.045(TBA) + 0.0065(AGE)

where ELV = elevation (m), MAP = mean annual precipitation (cm), TBA = total basal area (m^2/ha), AGE = mean age of oldest canopy layer (years), and adjusted $R^2 = 0.93$. The direction of the terms in this equation, negative MAP and TBA, and positive ELEV and AGE indicates the relationship between mean DMR and these four variables. It suggests that the most severe Douglas-fir dwarf mistletoe occurred in plots located in old, open stands on high, dry sites.

Discussion

Douglas-fir dwarf mistletoe occurred significantly more often in the white fir series than in the Douglas-fir series. This suggests that in the southern Cascade Mountains in Oregon, the presence of these climax series could be used to identify the relative frequency of Douglas-fir dwarf mistletoe at the landscape scale. Douglas-fir dwarf mistletoe also occurred significantly more often in plots on the highest, coolest, and driest sites within the white fir series. This suggests that high, cool, dry white fir plant associations might be useful indicators of the relative frequency of Douglas-fir dwarf mistletoe in the white fir series.

The trend for Douglas-fir dwarf mistletoe to be on sites at higher elevations and with lower mean annual temperatures mirrored the elevations and mean annual temperatures of the white fir series. The white fir series, which had the highest frequency of Douglas-fir dwarf mistletoe, occurs on higher, cooler sites than the Douglas-fir series, where the lowest frequency of dwarf mistletoe was found. Although not statistically significant, the only plot in the Douglas-fir series where the mistletoe was found was in the plant association with the lowest mean annual and dry season precipitation levels of all associations in the study. The frequency of occurrence of Dou-

glas-fir dwarf mistletoe in the western hemlock series was not significantly different from either of the other two series. Plots in the western hemlock series had a greater range of elevations and mean annual temperatures than the other two series, but tended to have higher mean annual and dry season precipitation. This suggested that the western hemlock series may encompass environmental conditions associated with both frequent and infrequent occurrence of Douglas-fir dwarf mistletoe. These trends are similar to those reported by Merrill and Hawksworth (1987). They found that the ecological factors associated with high frequency of southwestern dwarf mistletoe (*A. vaginatum* subsp. *cryptopodum* Engelmann) in Colorado were the same ecological factors associated with the habitat type where that mistletoe was most common. They concluded that the similarities in these trends are due to the fact that dwarf mistletoes are obligate parasites. Therefore, they are directly affected by environmental conditions and other ecological factors that affect their host.

The association between occurrence of Douglas-fir dwarf mistletoe and plots with significantly lower Douglas-fir basal area and smaller percentages of Douglas-fir was consistent with the higher frequency of mistletoe infection in the white fir and western hemlock series than the Douglas-fir series. Both the white fir and western hemlock series contained less Douglas-fir basal area and smaller percentages of Douglas-fir than the Douglas-fir series (Table 1). Acciavatti and Weiss (1974) found similar results in the White Mountains of Arizona, where the frequency of *A. microcarpum* Engelm. on Engelmann spruce *(Picea engelmannii* Parry ex Engelm.*)* was highest where it grew in mixed, rather than pure stands. However, pure stands of Engelmann spruce in the White Mountains are found at higher elevations than mixed stands, unlike Douglas-fir in our study area, which is found at lower elevations than the other conifer species. This suggests that in both cases, conditions that favor dominance by the host trees might be too extreme or otherwise unfavorable for the respective dwarf mistletoes.

Many plots throughout the study area had been disturbed by partial cutting of large Douglas-fir 10 to 50 years ago. Removing large trees can (1) stimulate latent dwarf mistletoe infections in understory trees by increasing light to the remaining crowns and (2) favor mistletoe spread by reducing stand density (Baranyay and Smith 1972, Parmeter 1978). Partial cutting in our study area appeared to be concentrated on shallower slopes accessible with ground equipment. Dwarf mistletoe-infected Douglas-fir were found more commonly on shallow slopes than on steep slopes. The mistletoe most likely was on site prior to disturbance, but would have been stimulated by it. We therefore speculate that partial cutting may have been largely responsible for the significant associations among Douglas-fir basal area, slope, and the frequency of occurrence of Douglas-fir dwarf mistletoe that we observed.

Douglas-fir dwarf mistletoe occurred most frequently on andesite and basalt-derived soils which are generally described as productive, deep and fertile. Soils derived from pyroclastic materials (where Douglas-fir dwarf mistletoe was least common) are young, shallow and infertile (Atzet and McCrimmon 1990).

At the beginning of the study, we anticipated that the Douglas-fir series would have the highest frequency of Douglas-fir dwarf mistletoe. Where Douglas-fir is the climax species it was expected that the presence of overstory and understory trees of the same species would facilitate spread of the mistletoe. In fact, the Douglas-fir series turned out to have the lowest frequency of the mistletoe. One factor that could be responsible for this is fire. In the southern Cascade Mountains in Oregon, the Douglas-fir series has historically been subject to more frequent disturbance by fire than any other series (Atzet and McCrimmon 1990). Surface fires of varying intensity are common and crown fires also occur (Agee 1993). Intense surface fires tend to destroy mistletoe-infected trees and crown fires eliminate both host and mistletoe from burned areas. Reestablishment of host trees usually occurs much more rapidly than re-invasion of mistletoe. This can result in large areas that are free of mistletoe for long periods of time (Alexander and Hawksworth 1975). In the Douglas-fir series, fire may have had an important role in limiting the frequency of Douglas-fir dwarf mistletoe. Fire may also have been a factor that prevented or eliminated Douglas-fir dwarf mistletoe infections in the three plant associations in the western hemlock and white fir series where no Douglas-fir dwarf mistletoe was found. Data from Atzet and McCrimmon (1990) indicates that fires were frequent in these two western hemlock associations

and infrequent but intense in the white fir association. If we continue suppressing fires in the future, Douglas-fir dwarf mistletoe could occur more frequently in the Douglas-fir series because once established it would infect each succeeding generation of Douglas-fir. However, after a very long time, frequency of *A. douglasii* in the white fir and western hemlock series might diminish because here Douglas-fir is a seral species and will gradually disappear if there is no disturbance.

Douglas-fir dwarf mistletoe was most severe on high, dry sites in the white fir and western hemlock series where the total basal area was low and where the age of the oldest canopy layer was greatest. These stand conditions are similar to conditions in which Tinnin et al. (1976) found isolated, severe infections of Douglas-fir dwarf mistletoe along the Cascade crest north of the study area. They hypothesized that these conditions may have provided refugia for the mistletoe because open conditions and sparse vegetation would have prevented most fires from carrying through those stands.

The relationship between increasing severity of dwarf mistletoes, decreasing basal area and increasing stand age is well documented (Merrill and Hawksworth 1987, Hawksworth and Johnson 1989, Mathiasen et al. 1990). A number of factors may account for these relationships. Stands with low basal area may be exposed to more sunlight, which would promote both shoot and broom development (Kuijt 1955). Open stands have higher levels of mistletoe seed production and greater opportunity for unobstructed seed flight among trees (Baranyay and Smith 1972). According to Parmeter (1978), in old trees with minimal height growth, mistletoe will advance in the crowns until the trees are completely parasitized.

Our study suggests that occurrence of the white fir and Douglas-fir series could be useful indicators of the relative frequency of Douglas-fir dwarf mistletoe at the landscape scale in the southern Cascade Mountains in Oregon. Since Douglas-fir dwarf mistletoe was most frequent in the white fir series, stands in this series may be the best candidates to manage as habitat for wildlife species that use Douglas-fir dwarf mistletoe brooms (Parks et al. 1999). However, where individual tree vigor and rapid growth are important objectives, stand structures and silvicultural regimes that favor dwarf mistletoe spread may be inadvisable. The significant increase in severity associated with decreasing basal area and increasing age raises concerns about partial cutting in portions of the study area where Douglas-fir dwarf mistletoe occurs. Partial cutting often results in stands with low basal areas and is often prescribed to retain or develop large, old trees. If these trees are infected, conditions would favor development of severe dwarf mistletoe infestations.

More information is needed on the underlying cause of differences in Douglas-fir dwarf mistletoe distribution observed today to understand the potential for the spread of infection in the future. Studies of site-specific fire history might provide information about the extent to which fire regulated Douglas-fir dwarf mistletoe distribution and severity in the past. If theories about the relationship between fire regimes and Douglas-fir dwarf mistletoe are correct, continued fire suppression may allow Douglas-fir dwarf mistletoe to become more common in areas where it is currently rare or absent. This would be of most immediate significance in areas of the white fir and Douglas-fir series that historically had frequent fires. Greater understanding of the interaction between fire and dwarf mistletoe infection is also needed to understand the impact of periodic prescribed underburning in dwarf mistletoe-infested stands.

Research is also needed on the differences in rates of spread and intensification of Douglas-fir dwarf mistletoe under various stand conditions before we can actively manage the level of infection to provide habitat for wildlife species that use Douglas-fir dwarf mistletoe brooms. The information gained from these and other studies will be useful to guide future management of the many stands with Douglas-fir and Douglas-fir dwarf mistletoe in the southern Cascade Mountains in Oregon.

Acknowledgements

We thank USDA Forest Service Pacific Northwest Region, Forest Health Protection Program for financial assistance for this project. Tom Atzet, Pat Martinez and Lisa McCrimmon, USDA Forest Service Area Five Ecologists, generously provided access to the data from their permanent plots and advice on study design and analysis. We also thank Don Goheen, Bob Mathiasen and Bob Tinnin for reviewing the manuscript and providing many useful comments.

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Received 24 February 1999
Accepted 12 August 1999

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Revisiting the Stock Concept in Pacific Salmon: Insights from Alaska and New Zealand

Introduction and Historical Perspective

Although systematists classify organisms by phylum, class, order, family, genus and species, it is widely appreciated that these are points along a continuum of genetic relatedness and evolutionary separation (Mayr 1982). This continuum extends to reproductively isolated breeding units within species, known to geneticists as demes and to most field biologists as populations. These populations may be spatially isolated from each other if they are on separate islands, mountaintops or in ponds. However, in many animals the isolation of populations is not a simple matter of geography and limited mobility but rather one of behavior. Many populations have broad, overlapping feeding distributions but segregate at the breeding season, each returning to the site where they were born. Among the most famous examples of this phenomenon are the anadromous fishes such as American shad (*Alosa sapidissima*) and salmon (*Oncorhynchus, Salmo* and *Salvelinus* spp.) (Quinn and Dittman 1992). These fishes are spawned in freshwater, migrate to sea to feed and grow, and then return to spawn, almost invariably in the same stream or lake where they were spawned.

Some astute scientists inferred the homing phenomenon in the 1800s from phenotypic differences in fish from different rivers. Milner (1876) noted "[t]he generally accepted fact in the habits of anadromous fishes that they are disposed to return to almost the exact locality where they passed their embryonic and earlier stages of growth... Observations of the shad brought to the large markets shows considerable difference in the physiognomy and general contour of those from different rivers. The suggestion is natural that they are distinct and separate colonies of the same species, and thus slight characteristics are perpetuated because they breed in-and-in and do not mix with those of other rivers." Others concluded from the isolated locations of salmon spawning groups that these must be fish returning to the location where they had been spawned. A report from the United States Commission on Fish and Fisheries (1876) stated, "This stream [near Elko, Nevada] is one of the many that form the headwaters of the Columbia River, and to this point, eighteen hundred miles from its mouth, the saltwater salmon come in myriads to spawn... From these facts we may infer that the instinct of location is probably sufficient to attract a colony of fishes as far inland as the headwaters of the longest

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river, whenever their home has been once established there."

Although homing is a fascinating phenomenon in its own right, the separation of the salmon species into more-or-less discrete populations is the key element in their management and conservation. The basis of this so-called stock concept is that salmon inhabiting different rivers experience different patterns of natural selection, owing to differences among rivers in abiotic factors such as flow regime, temperature and substrate, and biotic factors such as predators, competitors, prey and pathogens. These differences in selection result in salmon that differ in color, fat content, size, age, timing of migration, disease resistance, and many other phenotypic traits. Rivers may differ in the productivity of their salmon populations or their carrying capacity (Mobrand et al. 1997), thus the populations must be managed as separate entities to prevent over-fishing less productive populations when they intermingle with more productive ones. The connection between salmon homing, population-specific traits and conservation was the focus of a landmark symposium held in 1938 in Ottawa, Ontario, Canada (Moulton 1939). Several papers presented evidence for the population-specific traits of Atlantic and Pacific salmon (e.g., Rich 1939) and the published discussions make it absolutely clear that these scientists saw the close connection between homing, the stock concept, and salmon conservation.

The next major advance in the field of salmon population biology came with the publication of another symposium, also held in Canada, as part of the H. R. MacMillan Lectures in Fisheries at the University of British Columbia in Vancouver entitled "The Stock Concept in Pacific Salmon" (Simon and Larkin 1972). There were several interesting papers, but the volume is dominated by Ricker's detailed review of information on salmon homing, the differences among populations in various phenotypic traits, and the general failure of transplanted salmon to thrive as well as local populations (Ricker 1972). This outstanding review of the early literature is still widely cited today and was the key publication in the field until 1981, when a special issue of the Canadian Journal of Fisheries and Aquatic Sciences published papers from the Stock Concept International Symposium, held in 1980 in Alliston, Ontario. The issue had papers on a variety of fishes, including sea lamprey (*Petromyzon marinus*), largemouth bass (*Micropterus salmoides*), and walleye (*Stizostedion vitreum*), but many were on salmonids, including very useful reviews on Canadian populations of Atlantic and Pacific salmon by Saunders (1981) and McDonald (1981), respectively. As with the previous symposia, the authors clearly drew the links between homing, stock-specific variation in phenotypic traits, and the conservation and management of populations. In the years that followed this symposium, many papers were published, documenting variation among salmon populations in a wide variety of adaptive traits. Taylor (1991) reviewed much of the literature and pointed out that in some cases of "local adaptation," only phenotypic variation was documented. He argued that local adaptation implies not only phenotypic variation among populations in a given trait but also a genetic basis for the trait, and a demonstrated survival advantage associated with the trait.

In addition to the large and growing literature on population-specific variation in adaptive traits among wild salmon populations, the last few decades have seen rapid expansion of salmonid aquaculture. The successful culture of salmonids depended in part on the choice of suitable broodstock, and subsequent selective breeding for chosen traits. This requirement led to many experiments on the genetic control of traits of importance in culture such as fecundity and growth (e.g., Gjedrem 1983, Hershberger et al. 1990, Crandall and Gall 1993, Su et al. 1997, Jónasson et al. 1997). The general conclusion of these experiments is that there is a substantial genetic component to most of the traits, though of course there is a degree of environmental control as well. Finally, the 1970s and 1980s saw the development and use of molecular techniques to study the population genetics of fishes and especially salmon. These techniques initially used natural variation in the proportions of more or less selectively neutral polymorphic proteins to demonstrate reproductive isolation of salmon populations (see review by Utter 1991). More recently, variation in mitochondrial and nuclear DNA has also been used to study the population structure of salmon and other fishes (e.g., papers in the special issue of *Reviews of Fish Biology and Fisheries*, edited by Carvalho and Pitcher 1994).

Thus there have been three major lines of research into the subject of the "stock concept" or

evolution of salmon populations: natural variation in phenotypic traits, controlled or selective breeding, and variation in more selectively neutral molecular traits. As was pointed out in the 1994 American Fisheries Society symposium on "Evolution and the Aquatic Ecosystem" (Nielsen 1995, and notably Hard 1995), all are valid approaches and need to be integrated into a holistic view of salmon population structure, evolution and management (see also Utter et al. 1993, Grant et al. 1999). These lines of research, undertaken by scientists with diverse backgrounds and interests, form much of the scientific framework for the application of the U.S. Endangered Species Act to salmon populations (see discussions of this issue by Utter 1981; Waples 1991, 1995).

Taken as a whole, one can look at salmon populations from two perspectives. First, they have countless, genetically-based specializations for unique biotic and abiotic features of their environments. This perspective, bolstered by the general failure of anadromous salmonid transplants (Withler 1982, Fedorenko and Shepherd 1986, Harache 1992), sees salmon populations as tightly evolved for their natal systems, reinforced by nearly unerring homing behavior. The intermingling of populations may prevent management agencies from protecting the fine genetic structure but such structure exists. An alternative and perhaps complementary perspective (e.g., Quinn 1985, Wood 1995) is that since the post-glacial period, dispersal has been as much the hallmark of salmon population biology in the long run as homing. Following colonization of new habitat, subsequent homing isolates the nascent population. Natural selection and the high heritability of adaptive traits can lead to their rapid evolution. Differences in selectively neutral differences (e.g., molecular) traits may arise from founder effects at the time of colonization, or from drift over long periods of time.

Having presented this brief, and obviously selective, introduction to the subject of the stock concept in salmon, the purpose of this paper is to present studies supporting these two perspectives on the concept: fine-tuned adaptation or great capacity for evolutionary adaptation. The studies are drawn in large part from my own work, not because it is definitive but because it is familiar to me. It is not my objective to convince readers that either perspective is correct, but rather to emphasize the validity of both viewpoints.

What Constitutes a Population? Perspectives from Bristol Bay, Alaska Sockeye Salmon

The North American range of sockeye salmon (*Oncorhynchus nerka*) is primarily from the Columbia River to the Kuskokwim River in the Bering Sea (Burgner 1991). Early research by the International North Pacific Fisheries Commission revealed that Asian sockeye salmon (chiefly from the Kamchatka Peninsula and Russian coast of the Bering Sea) differed in marine distribution from North American conspecifics (French et al. 1976) and for some management purposes the continent of origin was the relevant scale for the "stock" (Figure 1, top; Harris 1987). However, data from tagging studies and analysis of naturally occurring parasites revealed that the distribution of sockeye salmon from the Bristol Bay region of southwest Alaska differed from those of other populations to the east and south (French et al. 1976). For example, the Fraser River complex of sockeye populations shows a different marine distribution (Figure 1, bottom), and also differs from Bristol Bay sockeye in survival rate patterns (Peterman et al. 1998).

Bristol Bay has some of the world's largest populations of sockeye salmon (Burgner 1991). These populations support important fisheries and have been the focus of much research, and in some contexts "Bristol Bay sockeye" is a meaningful stock or stock-complex. Despite the many lake systems tributary to Bristol Bay where adult sockeye salmon spawn, the adults generally return over a narrow time period (Burgner 1980). The populations also display coherent patterns of size at age and age at maturity (Rogers and Ruggerone 1993, Pyper et al. 1999), suggesting common responses to ocean temperature and density-related processes. Although for some purposes it is appropriate to speak of Bristol Bay sockeye, the management is based in districts at the mouths of the major river systems: Ugashik, Egegik, Naknek-Kvichak, Nushagak and Togiak, and to some extent these districts are functional stock units (Figure 2). As Minard and Meacham (1987) pointed out, this district-based management can lead to difficulties. For example, fishing in the Naknek-Kvichak district catches sockeye migrating to the myriad streams in the Naknek and Iliamna lake systems, and fishing in the Nushagak district intercepts fish with very different patterns

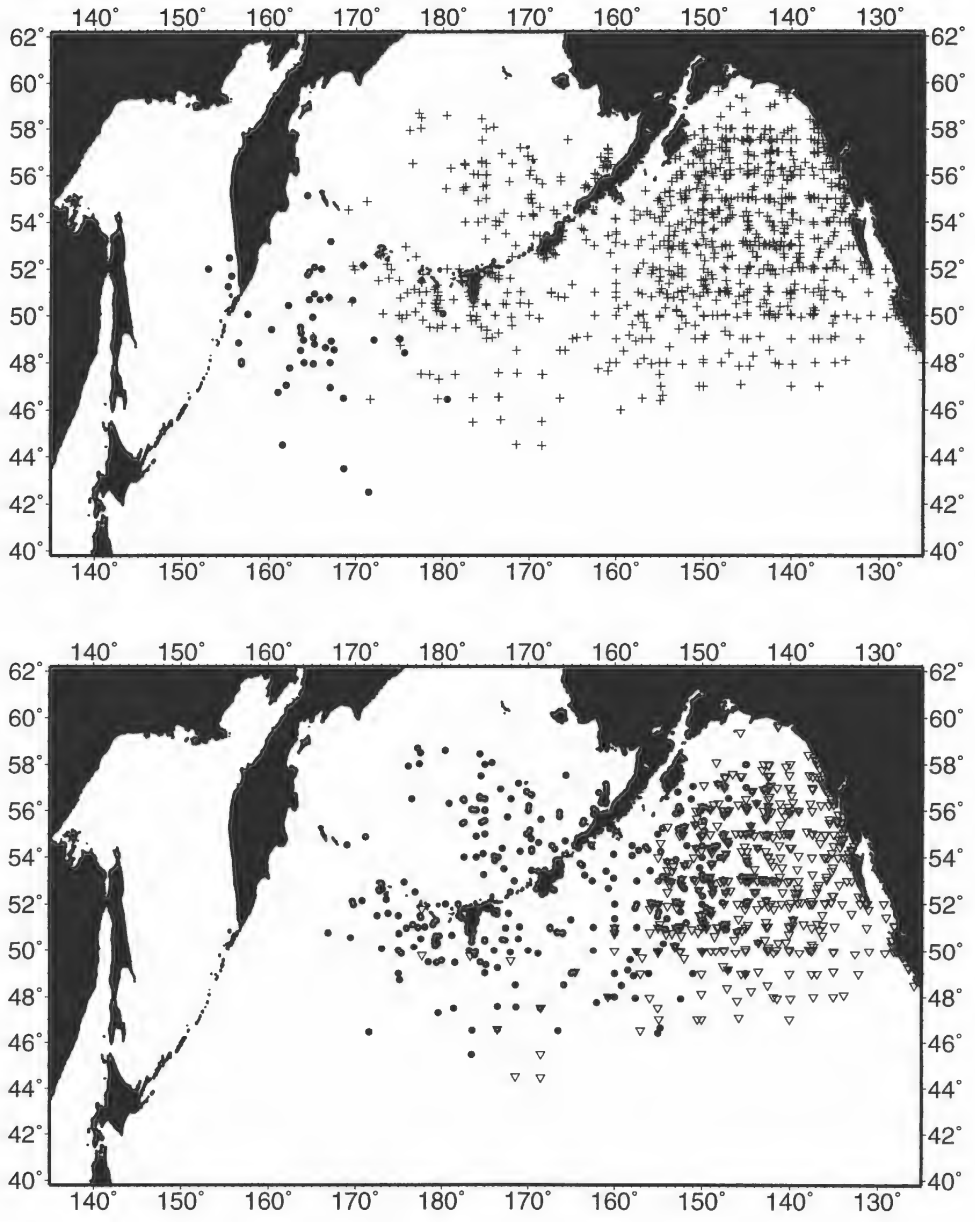

Figure 1. Locations at sea where sockeye salmon (immature and maturing) were tagged and subsequently recovered in coastal fisheries or spawning grounds. Top panel shows the distribution of sockeye recovered in Asia (solid circles) and North America (plus signs). Bottom panel shows the distribution of sockeye recovered in Bristol Bay (solid circles) and British Columbia (open triangles). Data should not be interpreted to indicate precise distributions or abundance, owing to uneven effort (source: North Pacific Anadromous Fish Commission data, map courtesy of Kerim Aydin, Fisheries Research Institute, School of Fisheries, University of Washington).

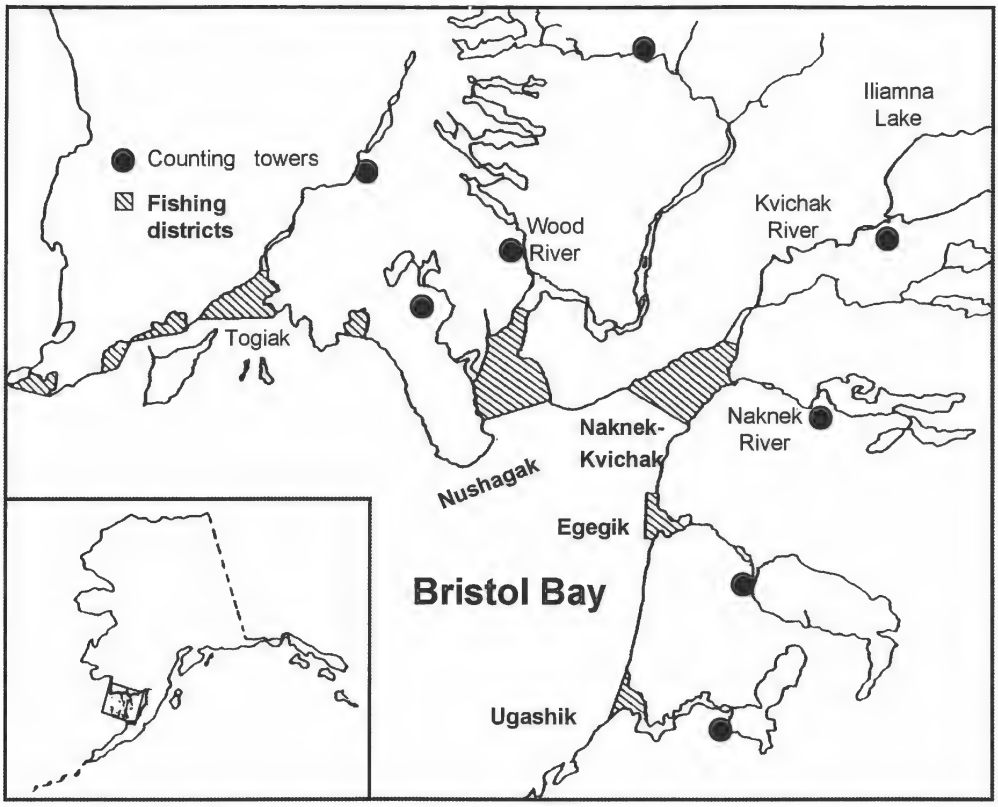

Figure 2. Map of Bristol Bay, Alaska, showing the fishing districts and locations of counting towers for sockeye salmon (modified from Minard and Meacham 1987).

of productivity and life history, going to discrete spawning sites in the Wood River, Nushagak, Nuyakuk and Igushik systems. There is always the danger of over-fishing one population while attempting to fully fish another. Efforts to avoid such management problems are complicated by the similar timing of the populations and the geographical proximity of their mouths. Counts of adult salmon migrating past towers such as the one at Igiugig on the Kvichak River provide in-season feedback for management (Minard and Meacham 1987) but still encompasses many spawning populations.

Even the fish migrating to a given river system may have very similar timing, as Smith (1964) and Jensen and Mathisen (1987) demonstrated for the Kvichak system. Sockeye tagged throughout the run were recovered at diverse spawning grounds in tributaries and beaches of Iliamna Lake and Lake Clark. Thus from the viewpoint of commercial fisheries management, the Kvichak River is the smallest practical unit, even though it encompasses about 100 documented spawning sites (Figure 3) and two of the largest lakes in Alaska (Demory et al. 1964). The Wood River system includes about 50 spawning populations associated with a complex chain of lakes (Marriott 1964). Like the Kvichak River system, it is also managed as one unit though estimates are made of the abundance of adult sockeye salmon at most of the spawning sites.

The sockeye salmon ascending the Wood River tend to spawn in three major types of habitats: small streams, large rivers (flowing between lakes) and beaches. Rogers (1987) pointed out the great variation in age structure among these groups.

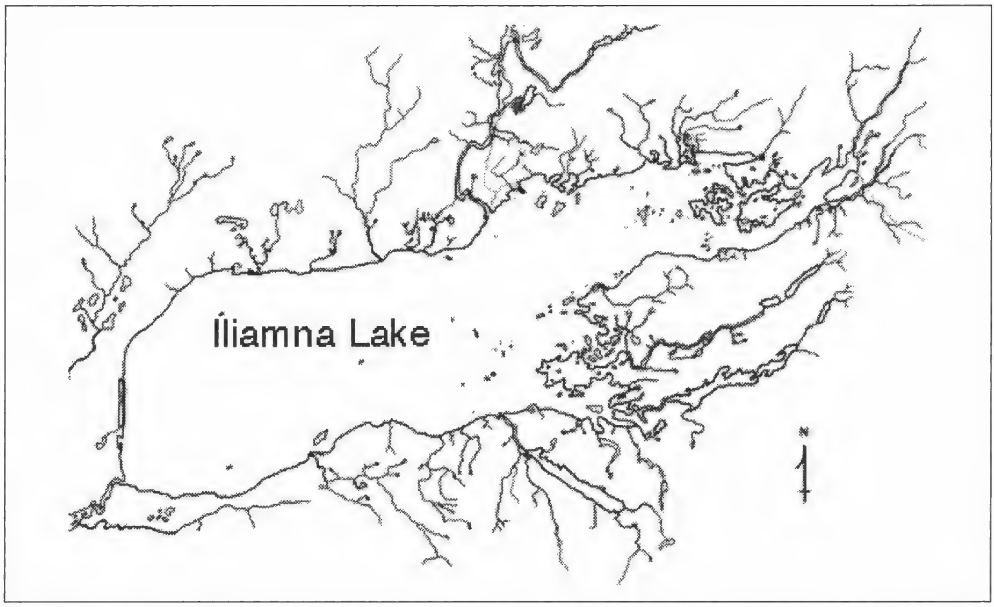

Figure 3. Map of Iliamna Lake, Alaska, showing some of the islands in the western part of the lake and the rivers that are used for spawning by sockeye salmon.

Notably, river spawners tend to spend three years at sea and so are larger than the creek spawners, which tend to return after two years at sea. The populations also differ in morphology, especially the development of the dorsal hump in males. Creek spawners are much less deep-bodied than river fish and the beach spawners are very deep-bodied (Bishop 1990, Wetzel 1993). The river and beach spawners in Iliamna Lake show parallel patterns of morphology (Blair et al. 1993) and these have been hypothesized (Blair et al. 1993, Quinn and Foote 1994) to result from the conflicting pressures of sexual selection (favoring deep bodies) and bear predation (Hanson 1992, Quinn and Kinnison, in press).

In Iliamna Lake, there are sockeye salmon spawning on beaches of low-lying islands, where the embryos incubate in water circulated by wind-driven surface currents. Only a few km away other females spawn on mainland beaches and spring-fed ponds supplied with upwelling water. The eggs deposited by females on the island beaches are exceptionally large whereas mainland beach and pond females have very small eggs, and these patterns of egg size match the size of the substrate in which the embryos incubate (Quinn et al. 1995). There have been no tagging studies to explicitly demonstrate homing by sockeye salmon to discrete spawning sites but natural variation in otoliths strongly indicates that sockeye return to their natal incubation sites (Quinn et al. in press). This finding is consistent with molecular genetic variation among spawning sites within this and other lake systems (Varnavskaya et al. 1994).

For some purposes we might think of the sockeye salmon spawning on the beaches of Iliamna Lake as a population because they clearly share many attributes such as egg size, fecundity, age and length at maturity (Blair et al. 1993). However, is there finer structure to the populations? Experimental displacement of mature salmon (Blair and Quinn 1991) and surveys of spawning dates (Quinn et al. 1996a) provide circumstantial evidence that the fish using each island represent separate populations. Not only is there apparently fine population structure on spatial scales but there is evidence for temporal isolation as well. Even within a single beach on one island, a certain section is always occupied prior to nearby areas (Hendry et al. 1995). The high heritability of maturation

date (Smoker et al. 1998) means that there may be patterns of genetic structure over the course of the spawning season within a single site (McGregor et al. 1998). The fish that arrive early in the season not only seem to live longer in the stream than late-arriving fish but also display different patterns of energy allocation (Hendry et al. 1999).

These studies of Bristol Bay sockeye salmon reveal a series of scales at which we may view populations: North America, Bristol Bay, Naknek-Kvichak or Nushagak fishing districts, Kvichak River or Wood River tower counts, spawning habitat types (beaches, creeks and rivers), individual islands or creeks, and even temporal segments of the run at a given site. Some scales such as continent or region are too coarse to be meaningful as populations and others such as creeks or segments of the run to a creek are much too fine to be manageable. Nevertheless, studies on the finest scale are useful because they reveal the extraordinary suite of adaptations that natural populations can display as evolved and phenotypically plastic responses to environmental variation.

How Rapidly Can Populations Evolve? Perspectives from Chinook Salmon in New Zealand

The almost endless ways in which natural populations differ from each other, and the complex adaptations to the environment that these differences seem to demonstrate, raise the question of how rapidly these differences can evolve. Much of the present range of Pacific salmon was last glaciated about 10-15,000 years ago, and strays founded the present populations. Thus not only homing but also straying is an important component of the life history and evolution of salmon (Quinn 1985). The differences in gene frequencies that are observed among populations have presumably accumulated gradually through genetic drift but selective breeding studies reveal high heritabilities for important life history traits and imply that populations might evolve quite quickly, given sufficiently intense natural selection.

Transplanted populations provide opportunities for studying the early stages of adaptation to new environments. There are countless introduced freshwater populations of salmon, trout and char worldwide but anadromous salmonids have proven very difficult to successfully transplant. This restriction is surprising because most population-specific differences seem to be adaptations for aspects of the freshwater environment (Taylor 1991) and one would think that marine life would be more generalized and so less problematical in new environments. Nevertheless, the transplant of chinook salmon from the Sacramento River (probably Battle Creek, Quinn et al. 1996b) to the Hakataramea River on the South Island of New Zealand (NZ) in the early 1900s was successful and the fish quickly colonized much of the suitable habitat and established self-sustaining populations in such large rivers as the Waimakariri, Rangitata and Rakaia (Figure 4), as well as smaller rivers.

Colonization must have been prevalent in the early years, given the rapidity with which the salmon distributed themselves, but present-day estimates indicate that the homing of NZ salmon is comparable to North American populations (Unwin and Quinn 1993). Examination of data collected over a period of years in several of the major chinook salmon rivers revealed differences in several of the life history traits commonly used to characterize chinook salmon populations in North America: freshwater life history type (yearling or subyearling migrants to sea), age at maturity, length at age, weight at length, fecundity, and the timing of return from the ocean and spawning (Quinn and Bloomberg 1992, Quinn and Unwin 1993). These differences indicated that the populations are now phenotypically different, though the extent to which these differences reflected only different rearing conditions could not be determined.

To determine whether chinook salmon have evolved into genetically distinct populations (in some sense of the word) during about 30 generations since the transplant (at a mean age of about 3), we initiated a large-scale controlled breeding and rearing experiment in 1994. The null hypothesis was that the fish from different rivers would not differ when reared under common conditions, implying that the differences in phenotypic traits observed in the earlier studies were environmentally induced. On the other hand, consistent differences between populations and genetic control (i.e., heritability) within populations would imply that the populations had already reached some level of genetic differentiation.

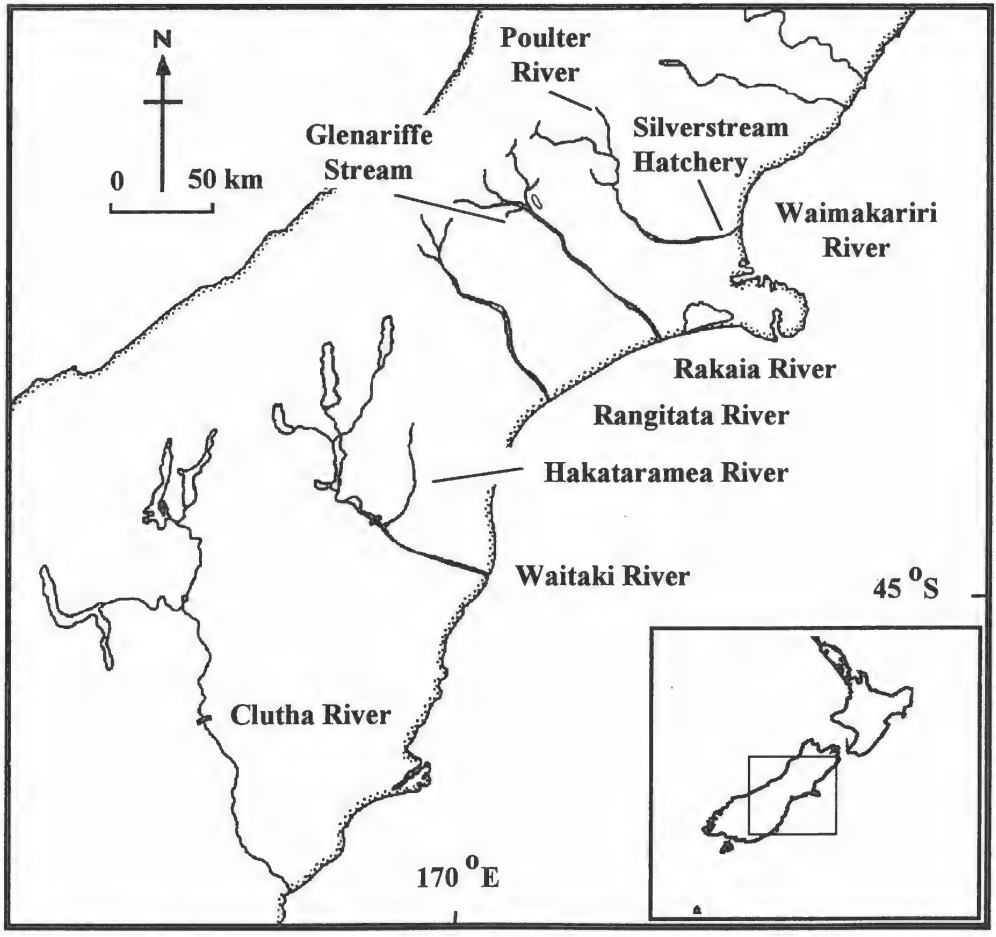

Figure 4. Map of the central South Island of New Zealand, showing the main chinook salmon rivers and locations of experimental facilities.

In 1994 and 1995, we sampled adult salmon from two populations that had shown phenotypic differences, the Hakataramea River and Glenariffe Stream, and recorded data on length, weight, age, morphology, egg size and fecundity. These phenotypic data were compared to data on fish from the current representatives of the ancestral Battle Creek, California population. We then spawned the NZ fish in a half-sibling mating design to allow us to estimate the genetic contribution to life history traits, and began a complex incubation and rearing experiment. We reared some families to maturity under common, controlled conditions in freshwater. In addition, we released representatives from the families from two different hatcheries (Glenariffe and Silverstream). The use of two hatcheries provided some measure of insurance against poor year class survival at one site and also allowed us to compare the performance of fish returning to one hatchery near the coast (Silverstream) and one farther inland and at higher elevation (Glenariffe). In 1997, we initiated another controlled breeding experiment, this time with fish from Glenariffe Stream and the Poulter River, the latter chosen because the adults differ from Glenariffe Stream fish in spawning date and juvenile life history.

Our results show a mosaic of traits, some of which are apparently under strong environmental control and others have a clear genetic basis and differ between populations. The adult chinook salmon differ in morphology from Battle Creek, California fish, and also differ (though to a lesser extent) between the two New Zealand populations (Kinnison et al. 1998a). We are presently examining the data on the offspring from the experimental NZ parents and so are not sure yet how much of the variation has a genetic basis. We have evidence that the temperature-specific rate of embryonic development does not differ between populations, despite differences between the rivers in thermal regime (Kinnison et al. 1998b). Salmon populations adapt the timing of juvenile emergence primarily by differences in parental spawning date, which is strongly heritable (our unpublished data) rather than developmental rate.

Growth rates differed slightly between Hakataramea River and Glenariffe Stream fish (Kinnison et al. 1998c) but the Poulter River fish grew much slower than Glenariffe Stream fish under common conditions (our unpublished data). This difference is particularly interesting because the Poulter River fish tend to spend a full year in freshwater prior to seaward migration whereas Glenariffe Stream fish rear in warmer water and typically migrate to sea in their first year of life (Unwin and Glova 1997). We infer that the fundamental environmental basis for growth differences between populations is becoming reinforced by a genetic difference as well. Smaller fish are less tolerant of seawater than larger fish (Kinnison et al. 1998c) and also have lower survival rates at sea (unpublished data) so there will be continued selection for fish in slow-growth environments to remain for a full year before going to sea – the life history pattern referred to as stream-type (see Teel et al. 1999 for insights into the evolutionary basis of stream-type and ocean-type life histories in North America).

Survival at sea was not only correlated with smolt size but there were also family-level differences independent of size, suggesting some genetic basis for survival. Survival is not a trait in itself but a consequence of many traits including growth, seawater tolerance, predator avoidance, etc. Perhaps most exciting was our finding that the two populations (Glenariffe and Hakataramea) showed similar survival rates when released from a site which was home to neither population (Silverstream) but that Glenariffe fish had a significantly higher survival rate than Hakataramea River fish when released from Glenariffe Stream. This "home site advantage" implies that some form of adaptation for the natal site has taken place that affects survival. Of the fish that survived and returned to the hatcheries, there is little evidence of inter-population differences in size at age, but we have detected consistent differences between populations in the timing of return and maturation, and also in female reproductive traits such as egg size. The energetic demands of upriver migration also seem to affect egg size, so the phenotypic traits seen in wild fish reflect the interplay between genetic and environmental controls. The genetic differences between populations in phenotypic (possibly adaptive) traits contrasts with the low level of variation among populations found using molecular markers within NZ, though the NZ fish differed from the Sacramento River fish (Quinn et al. 1996b). Further studies, using DNA microsatellites, are ongoing but it seems that selection has worked quickly on life history traits and drift may lead to differences, albeit small, in more neutral traits.

One additional finding, though not explicitly a goal of the study, was that many male chinook salmon held in freshwater became sexually mature at one year of age. This is not unprecedented, either in New Zealand or in the native range, but what was surprising was that they survived spawning and lived to spawn again, not only at age two but in some cases a third time at age three (Unwin et al. 1999). This illustrates that some aspects of salmon life histories, which we view as fixed, such as semelparity (i.e., death after reproduction), may actually be flexible but reveal only one pattern under normal environmental conditions. Another example of this phenomenon of apparently fixed traits that change in new environments is the age at maturity of pink salmon. Almost without exception they are two years old at maturity in their natural range but they have been reported to mature from ages 1-4 in the Great Lakes (Kwain 1987).

Conclusions

The population biology, genetics and conservation of fishes and salmon in particular is an exceptionally vital area of research, as revealed

by the diversity of papers in the American Fisheries Society symposium edited by Nielsen (1995), the set of papers in a special section of the journal Conservation Biology (Hedgecock et al. 1994), and the contributions of many scientists to a wide variety of other publications. I have tried to present two perspectives on the subject. In North America, we see stocks or populations defined over a range of scales, depending on the management goal and the tools of the scientists. We can observe differences in phenotype and often also genotype at spatial scales that may be too small for all be the most draconian fisheries management to actively protect. These myriad specializations are clearly critical to the health of salmon populations. In many cases there are obvious adaptive advantages to the traits, and failure of the vast majority of salmon introductions within and outside the natural range of the species also testifies to the importance of local adaptations.

How, then do we interpret the evidence from New Zealand that salmon can apparently evolve quite quickly? Does this mean that all we need to conserve are a few generic salmon stocks and we can use them to replenish any habitat from which salmon are lost? Or does their rapid evolution demonstrate how critical the local adaptations are to the fitness of individual salmon and the productivity of populations? The scientists and policy makers wrestling with the application of the U.S. Endangered Species Act to "distinct population segments" have a very difficult job, weighing the various attributes that define populations (Utter 1981, Waples 1991, 1995). They must rely on different kinds of data, including molecular markers, life history traits, and geology (e.g., Myers et al. 1998) to define the "evolutionarily significant units" that society will try and protect, and must deal with criticisms of the ESU concept (e.g., Pennock and Dimmick 1998). My own view is that there are some populations with unique attributes and we should strive to protect them but for the most part we need to give salmon access to healthy, diverse physical habitats and allow those habitats to be filled (or over-filled) with the full community of salmonid species native to the region. The salmon can take it from there.

Acknowledgements

The research conducted on Bristol Bay sockeye salmon that I have described has been largely supported by the Pacific Seafood Processors Association. I am very grateful to Don Rogers of the Fisheries Research Institute, School of Fisheries, University of Washington, for his insights into the salmon of that region, and the opportunity to participate in the research program there, and I thank the many graduate and undergraduate students who helped with the work. The research on chinook salmon in New Zealand has been a collaborative effort with Martin Unwin and Nelson Boustead of the National Institute of Water and Atmospheric Research, and Michael Kinnison and William Hershberger of the School of Fisheries. I thank the many staff associated with fish husbandry at Glenariffe and Silverstream, and with sample processing throughout this study. Funding was provided by the New Zealand Foundation for Research, Science and Technology (Contract C01501 in New Zealand), and by a consortium of Pacific Northwest power utilities and the H. Mason Keeler Endowment (in the U.S.). Martin Unwin, W. Stewart Grant and Fred Utter provided helpful comments on the manuscript.

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Book Reviews

Biology and Management of Noxious Rangeland Weeds

Edited by Roger L. Sheley and Janet K. Petroff, Oregon State University Press, Corvallis, OR, 438 pages, ISBN 0-87071-461-9 ($39.95)

Biological invasions are perhaps the single most important ecological problem facing what remains of native ecosystems in North America. Their effects may be a greater threat to ecosystems than the potential loss of single endangered species. They represent the potential to change the structure and function of ecosystems, rendering entire landscapes uninhabitable for native species.

Noxious weed invasions on western rangelands is not a new issue. Perhaps the first, and likely the most significant, biological invasion on western rangelands was cheatgrass (*Bromus tectorum*). However, a number of more recent invaders have begun to make their mark on rangelands and forests across the western United States. The economic and ecological impacts of these invasions are now being felt by range managers.

Sheley and Petroff have assembled more than fifty authors representing academia, private industry, extension, and county, state and federal research and land management agencies. Their goal is to provide a comprehensive text on rangeland weed management for natural resource students and practicing land managers. The book attempts to bridge the gap between weed science and weed management with much of the emphasis on planning. Geographically, the book covers Arizona, California, Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oregon, South Dakota, Washington and Wyoming in the United States, and Alberta, British Columbia, Manitoba and Saskatchewan in Canada.

The book is organized into two sections. Section I covers theory and principles of weed management. Much of this section is devoted to comprehensive weed management planning. Specific topics covered include inventory, economic evaluation, prevention, early detection and eradication, grazing effects, biological control, herbicide use on rangeland, and revegetation. These chapters provide a wealth of information on the breadth and depth of issues that must be considered in a weed management plan. There does not appear to be any attempt to provide a "cookbook" for planning, but rather to provide managers with an introduction to each topic and how they relate to weed management. They also provide additional references to guide the reader to more detailed information if needed.

The editors' primary focus is on the technical aspects of weed management. However, the chapter on coordinated weed management planning provides a valuable introduction to the changing face of natural resources management planning. Weed management can be as controversial as any other aspect of natural resource management. This chapter provides an introduction for those of us trained only in the technical aspects of natural resource management to the basic procedures for stakeholder involvement in policy development and planning. The author focuses on the importance of the planning *process* in achieving consensus and avoiding conflict. This is especially important in light of the changing social goals (economic activity vs. environmental quality) for public lands.

Section II covers specific management aspects of twenty-nine weeds of particular concern to land managers in the west. Sheley and Petroff include in this list not just regulatory noxious weeds, but also others with invasive characteristics such as cheatgrass. The chapters for each weed species include sections on identification, origin, history and distribution, potential for invasion, impacts, biology and ecology, and management. These chapters provide species specific details of prevention, control and eradication methods proven to be effective. They provide information on the specific conditions under which these methods will work, the results that can be expected and an indication of the level of effort required to reach management goals for each species.

Overall, the book meets the editors' goal of providing a resource for land managers in the fight against noxious weeds. Section I successfully

provides the reader with an appreciation for the complexity involved in developing a weed management plan. The detailed chapters on each weed species in Section II appear to be thorough and authoritative.

As in any book of this type, the large number of contributors are both its greatest strength and weakness. Although the editors acknowledge each chapter is written by different authors and their styles may vary greatly, there are some differences in terminology, usage and level of detail between authors that may be confusing to readers new to the topic. These weaknesses are far out-weighed by the breadth of viewpoint and expertise brought by the large number of authors. In the theory and concept sections, they provide a variety of perspectives and situations that will greatly assist the reader identify his/her own weed management problem and/or potential solution. Because so many of the authors are authorities in research or implementation of the concepts presented, the reader is provided with the most up-to-date information. This book will undoubtedly be used by many students and land managers across western North America as the most comprehensive resource compiled to date on rangeland weed management.

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NORTHWEST SCIENCE

Information for Authors

Scope of Articles

The pages of *Northwest Science* are open to original and fundamental research in the basic, applied, and social sciences. *Northwest Science* does not generally publish notes or review articles. All submissions are refereed, usually by two reviewers. Papers are welcome from authors outside of the Pacific Northwest, but at least one author of any paper considered for publication must be a member of the Northwest Scientific Association.

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Ceska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia University Press, New York.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. *In* H. Barnes (ed.) Proceedings of the 9th European Marine Biology Symposium, Aberdeen University Press, Aberdeen. Pp. 363-393.

Theses, dissertations, personal communications, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary pons in Alberta. University of Calgary, Calgary. M.S. Thesis.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. University of Utah, Salt Lake City. Ph.D. Dissertation.

Danwiddie, P. W. In Press. Dichotomous key to conifer foliage in the Pacific Northwest. Northwest Science.

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Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agricultural Experiment Station Technical Bulletin 60. Washington State University. 210 p.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA Forest Service Research Paper RM-214. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. 39 p.

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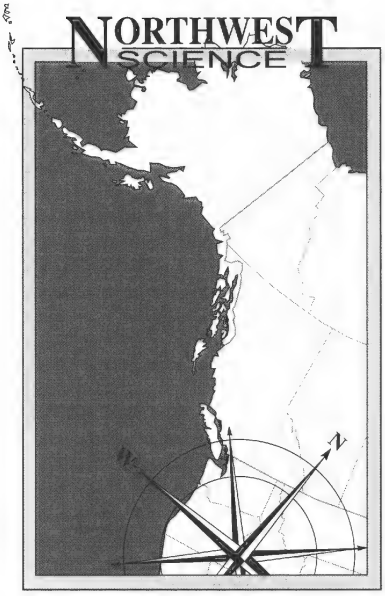

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Quarterly Publication of the Northwest Scientific Association

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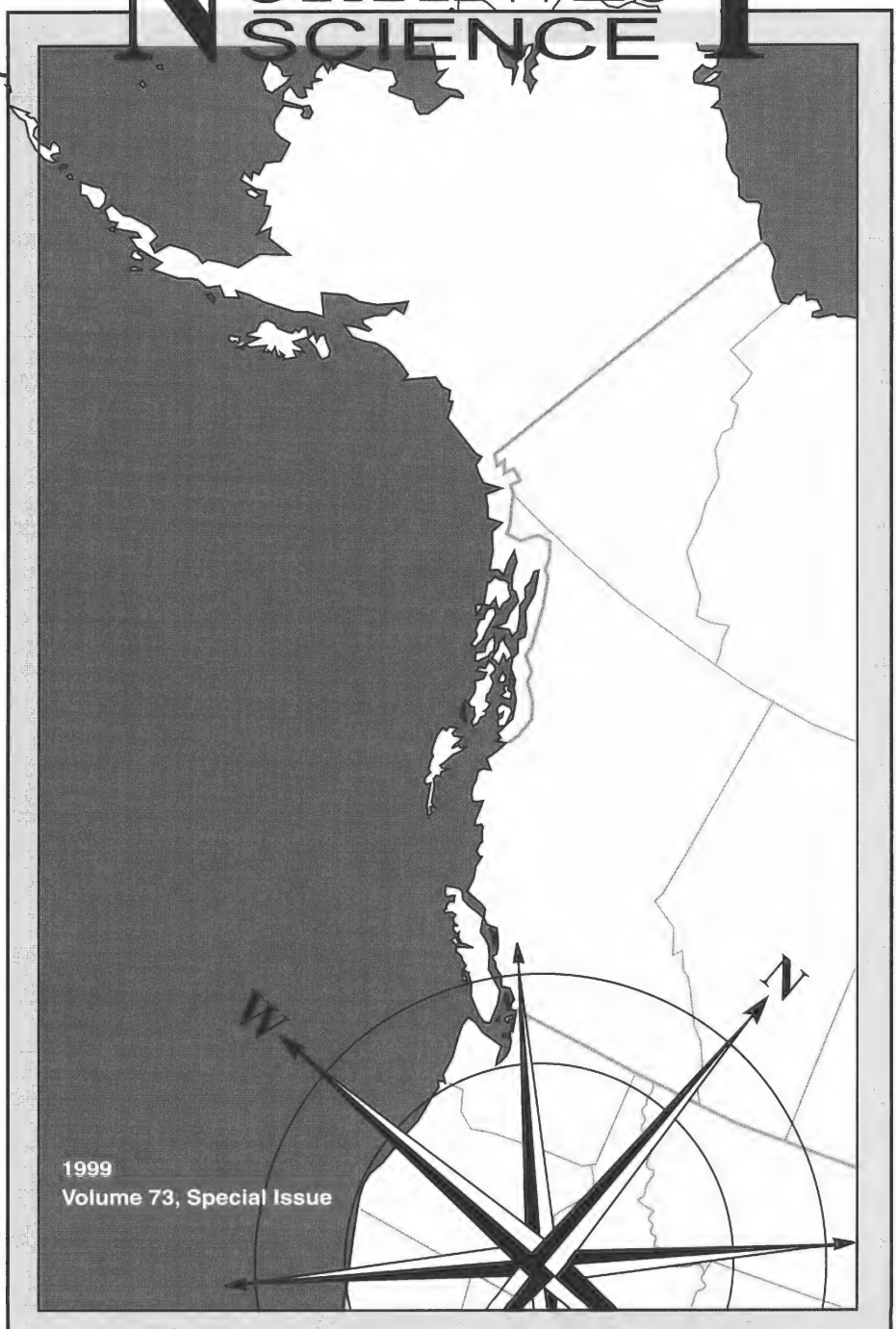

1999
Volume 73, Special Issue

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(Founded 1923)

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1999 Volume 73, Special Issue

NORTHWEST SCIENCE

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ISSN #0029-344X

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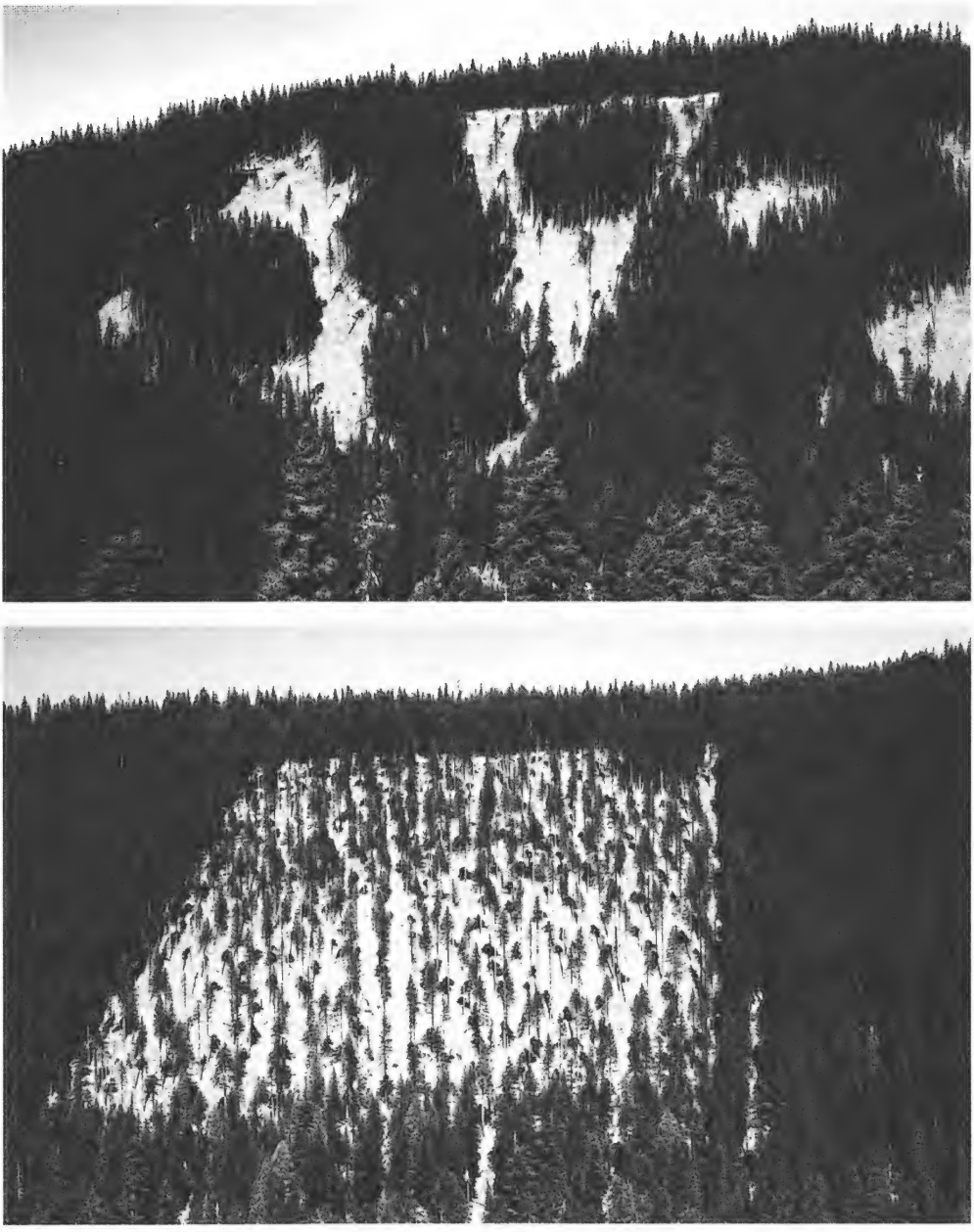

The Demonstration of Ecosystem Management Options (DEMO) study examines the resopnses of diverse groups of forest organisms and processes to varying levels and patterns of retention of live trees through harvest. These photos illustrate three of the six 13-ha experimental treatments at the Dog Prairie block (Umpqua National Forest)—one of eight study sites in western Oregon and Washington. The treatments shown are: 75% aggregated retention (top photo, right), 40% aggregated retention (top photo, left), and 15% dispersed retention (bottom photo). (Photograph by Charles B. Halpern).

Special Issue on Retention Harvests in Northwestern Forest Ecosystems: The Demonstration of Ecosystem Management Options (DEMO) Study

Preface

Large-scale, long-term field experiments are necessary to understand the ecological consequences of forest management policies and practices. Despite widespread recognition of their value, however, few such studies have been undertaken. There are numerous impediments to experimentation at large spatial and temporal scales: access to experimental sites of sufficient size or number, operational and logistical constraints associated with large-scale field manipulation and sampling, and the high cost and limited mechanisms for sustained funding of long-term research. In addition, the underlying goals and approaches of scientists and resource managers can differ substantially. Thus, to succeed, large-scale, long-term experiments that address resource management issues must reflect both standard scientific conventions and the practical goals and constraints of forest management.

This Special Issue of Northwest Science contains a series of nine papers devoted to a large-scale, long-term, interdisciplinary study of the ecological and silvicultural effects of green-tree (or structural) retention harvests on federal forest lands in the Pacific Northwest: the Demonstration of Ecosystem Management Options (DEMO) study. Forest management practices on public lands have changed significantly in the last decade in response to growing concerns that traditional approaches—clearcut logging and plantation forestry in particular—have led to widespread loss and fragmentation of old-growth ecosystems and to increased risk to persistence of organisms associated with late seral forests. New standards and guidelines contained in the Northwest Forest Plan specify the minimum levels and spatial patterns of live trees and coarse woody debris that must be retained on those lands subject to timber harvest (i.e., Matrix lands and Adaptive Management Areas). Although these recommendations represent the current scientific literature and the collective knowledge and professional judgements of the biologists and ecologists who contributed to the Northwest Forest Plan, the ecological consequences and social perceptions of alternative harvest strategies have not been rigorously tested. The DEMO study is among the first to examine, experimentally and over a wide geographic area (western Oregon and Washington), the responses of diverse groups of forest organisms and processes to variation in the amount and/or pattern of live trees retained through harvest.

The papers contained in this Special Issue discuss

- the evolution of the DEMO study and the social and political context within which it developed;
- the experimental design, harvest prescriptions, and study sites;
- the nature of the component investigations, including hypothesized responses and unique findings from pre-treatment sampling; and
- the challenges faced and lessons learned during the design and implementation of the experiment, from the perspectives of the scientists and managers involved.

Despite the numerous impediments to large-scale, long-term, and interdisciplinary research, the scientists and managers who have participated in DEMO have been successful in initiating a broadly replicated and comprehensive experiment. A major goal of this publication is to encourage new and collaborative research participation in the study. At the time of publication, harvest treatments

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have been completed at six of the eight experimental blocks; a first assessment of early, post-harvest responses will extend into the year 2001. There remain numerous opportunities to take advantage of the experimental design and of the comprehensive set of baseline data to design additional organism-, community-, or process-based studies. Experimental manipulations of forest ecosystems at this scale provide a rare and invaluable resource.

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The History of DEMO: An Experiment in Regeneration Harvest of Northwestern Forest Ecosystems

Abstract

As management priorities for federal forest lands have shifted, it has become clear that different strategies for harvest and forest regeneration are needed. The DEMO experiment arose in response to this need, with leadership provided by a consortium of university and Forest Service scientists and federal forest managers. With specific congressional direction (included in federal appropriations for the Forest Service), the initial planning for an experiment in retention harvest strategies began in 1992. Initial planning efforts were hampered by competing research objectives and disagreements over experimental design, shifts in program leadership, difficulties in transferring funds to the appropriate entities, and conflicts related to the Federal Advisory Committee Act. In 1994, once these challenges were overcome, the experiment began.

DEMO is not only an experiment in retention harvesting, but also in collaboration between research and management, as well as federal and state governments and the university community. The scope and intensity of collaboration have been demanding, requiring effective communication and coordination across institutional lines. The early history of DEMO has taught us that experiments of this kind require: (1) a coordinated legislative package and multi-year budget commitment, (2) a well-developed management structure, (3) an efficient process for planning, (4) commitment of lead scientists to the coordination and planning of disciplinary and interdisciplinary research activities, (5) effective collaboration between research and management, and (6) a well-developed outreach program. Other large-scale silvicultural/ecological experiments with characteristics similar to DEMO are underway at several locations around the world. These will offer additional learning opportunities for large-scale, interdisciplinary research.

Introduction

A common perception of traditional resource management is that it is based on scientific experimentation. In this paradigmatic view, scientific findings in the fields of soil science, ecology, and plant physiology are used to formulate management approaches that are tested prior to widespread application.

Yet such a systematic approach to forest management has been rare—at least in North America during the 20th century. For example, there has never been a credible, large-scale, statistically designed experiment in regeneration harvest of Douglas-fir forests of the Pacific Northwest. Dispersed patch clearcutting adopted on national forests in the Pacific Northwest after World War II was consistent with the findings of Isaac (1943) and others; however, the concept was applied extensively without experimental testing. Alternative approaches, such as selection cutting, were rejected based on a few case studies. Other harvest experiments were done at a very small scale and generally lacked statistical rigor, especially statistically valid replication; Tappeiner et al. (1997) provide a more comprehensive review of the evolution of harvesting methods in the region.

New societal demands and increased scientific knowledge are driving major changes in forest management which require integration of ecological values (such as maintenance of biological diversity) with commodity production (Kohm and Franklin 1997). Under intense scrutiny from interested stakeholders, managers are faced with developing and applying new, unproven approaches to forest management. Although presumably based upon the best available science, the economic and ecological costs, benefits, and overall effectiveness of these new approaches are unknown. This is the case on federal, state, and private forest lands in the Pacific Northwest (e.g., Tuchmann et al. 1996).

The new paradigm for testing such approaches is called *adaptive management*—although in a less

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formal form, the concept has existed for several decades. Adaptive management calls for the systematic and iterative collection of information to assess and, where necessary, modify policies and management strategies. Science is an important part of this process. Yet, experiments which involve large treatment areas and long periods of time are difficult to establish and maintain.

In this paper, we describe the evolution of a major experiment in retention harvesting, the Demonstration of Ecosystem Management Options (DEMO) study. We describe the origin of the experiment, the role of an institutional partnership (New Perspective Partners) in obtaining congressional support, and the development of the experimental design through several iterations. Our objective is to share lessons with others who become involved in such projects. Finally, we identify other large-scale, silvicultural experiments to illustrate the range of large-scale experimentation in modern resource management. These experiments (including DEMO) reflect an increasingly common blend of research and management that is essential to the implementation of ecosystem management.

Conception and Early History

The need to examine the effectiveness of alternatives to traditional silvicultural regimes, such as clearcutting, has been recognized among foresters and scientists for several decades (e.g., Hammond 1991). The northern spotted owl debate (see, e.g., Thomas et al. 1990) and other issues related to biological diversity and ecosystem functions, such as hydrologic regulation (see, e.g., Jones and Grant 1996), intensified interest in alternative silviculture during the 1980s. Concurrently, our understanding of ecosystem structure and function (e.g., Franklin 1992), natural disturbances (e.g., Franklin et al. 1995), and the consequences of large-scale manipulation of forest landscapes, such as fragmentation (e.g., Franklin and Forman 1987), expanded dramatically.

In 1991, there was an opportunity to establish a major harvest experiment that would integrate ecological and commodity objectives on the Olympic Peninsula of Washington State. In 1989, the Commission on Old Growth Alternatives for Washington's Forest Trust Lands recommended creation of a new research facility, the Olympic Natural Resources Center (ONRC), as well as an Olympic State Experimental Forest (OSEF) to be created from a large block of trust lands managed by the Washington Department of Natural Resources (WDNR). Development and testing of silvicultural approaches that integrate wildlife (including the spotted owl) and fish values with commodity production were a high priority objective of the experimental forest.

A major forest harvest experiment was proposed as a potential "flagship" activity for the newly established ONRC. This experiment would not only address a major research need, but also serve as a focal point for creating an interdisciplinary, inter-institutional environment for research on the Olympic Peninsula. Design work was initiated in December 1991 by Dean R. Berg, then a staff member of ONRC, and Jerry F. Franklin. WDNR staff in Forks and Olympia were included in discussions from the onset.

A detailed plan was completed in May 1992 after review of preliminary designs by scientists and staff from the ONRC, WDNR, and USDA Forest Service Pacific Northwest Research Station in Olympia, Washington. The plan called for a split-plot design involving eight structural treatments and two logging systems (readers unfamiliar with the concept of retention harvest methods and related concepts, such as aggregates, are referred to Franklin et al. 1997). The treatments initially were: (1) 0% retention (clearcut); (2) 12% retention in dispersed and aggregated fashion, respectively; (3) 24% retention in dispersed and aggregated fashion, respectively; (4) 60 and 80% retention, with harvest in the form of group selection; and (5) untreated control. Response variables included tree growth and yield, understory composition, tree regeneration, animal communities, fungal communities, and the sources and dynamics of coarse woody debris. A simplified plan involving only six treatments eventually emerged from this scoping effort (Olympic Natural Resources Center 1992).

Extensive discussions between ONRC and WDNR staff continued with regard to location, particularly whether plots should be placed in second-growth forests of the Clallam River drainage or in old-growth forests elsewhere in the proposed OSEF. Differences in opinion reflected both scientific issues (e.g., homogeneity or levels of comparability among treatment areas) and policy. One manager opined, for example, that "Much

research is being conducted on mangling [sic?] second growth forests. Some should occur on the OSEF. . . . [however] the Department's prime interest in research is in finding ways to produce commodities from these old growth forest [sic] while at the same time protecting the ecological values."[1] No consensus was reached, and WDNR chose not to proceed with the experiment at that time.

Enter the New Perspectives Partners

Early in the 1990s, it became apparent that implementation of ecosystem management was hampered by lack of research—especially research integrated with management. While strong research programs existed in the region, they were poorly coordinated and disjointed with management—in some cases, researchers and managers worked at cross-purposes. In an effort to minimize such problems, the Ecosystem Management Partnership was formed (the name was changed later to New Perspectives Partners). New partners were added, but the originating institutions and individuals remained active, providing the leadership and continuity.

Initially the partnership included scientists from University of Washington, Oregon State University, the USDA Forest Service Pacific Northwest Research Station, innovators from the Aerial Forest Management Foundation, and resource managers from the USDA Forest Service Pacific Northwest Region. The group proposed a coordinated effort in ecosystem management research and development, as well as a mechanism for funding. Based on their work, specific federal appropriations were made to support ecosystem management research and development at the three research institutions and the Aerial Forest Management Foundation.

Working with members of Congress, the partners emphasized the need for experiments on alternative approaches to forest harvesting and suggested how such studies might be implemented on federal and state lands in the Pacific Northwest. At the same time, the Douglas Project Coalition (a local group of interested businessmen and citizens from Douglas County, Oregon) was also seeking funding for a large-scale study and demonstration on the biological, social, and economic consequences of diverse forest management strategies.

The 102nd Congress quickly responded. On June 29, 1992, the House Committee on Appropriations reported the "Department of Interior and Related Agencies Appropriation Bill, 1993," which provided for establishment of silvicultural experiments on National Forest land (U.S. House of Representatives 1992). Language in this bill (under the timber sales section of the National Forest Systems appropriation) called for ". . . An increase of $1,000,000 in silvicultural examination. These funds, along with $1,000,000 in base funds to be redirected for this purpose, are to be provided for the Pacific NW New Perspective Partners demonstration program. These funds will be used, under the joint control of the scientists directing the program under the Forest research program and the NFS managers involved, to support scientific costs associated with the establishment of one major silvicultural experiment each in Washington and Oregon, using new forestry and landscape management techniques."

In the final version of the Appropriations Act for Fiscal Year 1993, Congress combined funding requests from the Olympic Natural Resources Center and Douglas Project Coalition into a $1.5 million earmark, directing the Forest Service to conduct demonstrations in consultation with the Partners and Douglas Project Coalition. Key congressional members behind this provision included: Sid Yates (IL) (then chair of the appropriation subcommittee which handled Forest Service budgets), Norm Dicks (WA), Les Aucoin (OR), Sid Morrison (WA), and Peter DeFazio (OR), and in the Senate, Mark Hatfield (OR).

Developing the Experimental Design

With direction and financial support from Congress, planning for the experiment began in earnest. In December 1992, the New Perspectives Partners' Scientific Coordination Team produced a consensus document on the form of the experiment. Their design emphasized a broad range of levels of green-tree retention with the pattern of retention (i.e., dispersed vs. aggregated) secondary. The design was similar to that developed earlier by ONRC, but it contained seven treatments. Levels of retention were increased in several of the treatments (e.g., from 12 to 20% and 24 to 40%) reflecting federal forest land managers' interests in higher levels of retention. Twenty hectares (50 acres) was suggested as the minimum treatment

area. Numerous response variables were identified including physical, biological, and economic parameters.

Subsequent analysis indicated that, due to limited availability of field sites, only six treatments were possible. Finding even the 180 ha needed for a single replication of six treatments of comparable forest stands and site conditions proved difficult. No suitable sites were found on the Olympic National Forest, originally planned as the locale for DEMO in the state of Washington; hence the experiment was shifted to the Gifford Pinchot National Forest where sites for three replications were ultimately found (Aubry et al. 1999, Halpern et al. 1999). An additional Washington replicate was sited on Department of Natural Resources Land, largely through the efforts of Washington Commissioner of Public Lands Jennifer Belcher and Gifford Pinchot National Forest Supervisor Ted Stubblefield. Sites suitable for four replications of the experiment were identified on the Umpqua National Forest in Oregon, partially due to the interests of the Douglas Project Coalition; Forest Supervisor Don Ostby was critical in this successful siting effort.

Next, research foresters at the USDA Forest Service Pacific Northwest Research Station in Olympia, Washington conducted much of the detailed design work on DEMO through 1993. A new design emerged that incorporated a full range of retention levels but substantially modified the treatments previously proposed:

Treatment	*Description*
0%	clearcut
20%	retention in small patches or aggregates (= clearcut with undisturbed patches)
40%	20% as aggregates and 20% as dispersed retention over the remaining 80% of the harvest unit (= shelterwood with undisturbed patches)
60%	created by cutting small patches occupying 20% of the area and thinning the remainder of the stand (= group selection with thinning)
80%	created by cutting small patches occupying 20% of the area (= group selection)
100%	uncut control

Although this design was clearly tied to traditional regeneration harvest practices, it was confounded experimentally in that levels and patterns of green-tree retention varied simultaneously, precluding the possibility of ascribing treatment-level differences to the amount or spatial patterning of retention. This was viewed as a serious issue by participants who wished to systematically examine responses to individual treatment variables. Indeed, a great deal of silvicultural experimentation can be criticized for its focus on comparisons of generalized silvicultural systems, such as shelterwood and selection, rather than on systematic manipulation of a single variable, such as tree density or spatial pattern of harvest. Such comparisons, which typically involve simultaneous manipulation of several variables, strongly limit the forester's ability to draw general inferences about the effects of manipulating forest structure.

Resolution of alternative experimental approaches occupied much of the spring of 1994. Two conceptually distinct approaches were proposed and debated: a comparison of specific silvicultural prescriptions in which several aspects of retention varied simultaneously (the design described above), or a systematic comparison of variation in levels and patterns of retention. Input from biometricians and quantitative scientists was critical in these discussions. The debate culminated in a meeting on May 2, 1994. Participants in DEMO made the decision to proceed with a design that allowed for clear statistical inferences regarding the effects of level and pattern of green-tree retention (see Aubry et al. 1999). The treatments included: 15% retention, dispersed; 15% retention, aggregated; 40% retention, dispersed; 40% retention, aggregated; 75% retention, aggregated; and 100% retention (control).

The first four treatments provide for a simple factorial comparison of two levels and two patterns of retention, and the last represents an untreated control. The nature of the fifth treatment generated significant debate. Some suggested 0% retention (a clearcut), whereas others preferred a treatment that represented a high level of retention. This issue was discussed at length, with National Forest System managers providing the deciding vote for 75% retention. At issue was whether a clearcut treatment could or should be applied on National Forest lands (since this prescription was no longer used), as well as a desire to experiment with higher levels of retention. The discomfort of many National Forest personnel was accentuated by the knowledge that they had no control over where the 0% retention treatment would be placed since it was to be randomly assigned. Of course, scientists often have used experimental treatments outside the bounds of

standard operational practices to provide tests of treatment variables that are sufficiently extreme to define the limits of the responses—i.e., to define the response surface. However, it was jointly decided by the managers and scientists involved in DEMO not to do so in this case.

Even though the original design work for DEMO preceded the work of the Forest Ecosystem Management Assessment Team (1993), the final DEMO plan considered the needs of, and was an appropriate response to, the Northwest Forest Plan, providing a rigorous evaluation of the individual effects of various levels and patterns of green-tree retention. As described in the final study plan for DEMO, "The DEMO design is expected to provide reliable and broadly applicable information on the effects of green-tree retention in harvest units, as well as information on disturbance responses and resource interrelationships in managed forest stands" (Anon. 1996). Of course, to ensure the "cleanest" test possible of the main variables of interest (level and pattern of green-tree retention), some other provisions of the Northwest Forest Plan (e.g., requirements for riparian buffers) were not implemented on the harvest units. The Plan allows for such deviations when necessary for a scientific experiment of this sort.

Lessons for the Future

DEMO has provided valuable insights into the initiation, development, and implementation of large-scale, multidisciplinary research—particularly research that stems from problems in natural resource policy and intimately involves those charged with its implementation. We have learned many lessons, although we have only just completed pre-treatment sampling, with harvesting underway at some locations. These lessons are most relevant to public sector projects (such as DEMO), but the principles are broadly applicable:

1. ***A coordinated legislative package.*** Typically, research is conducted independent of resource management (although clearly intended to address its needs). Efforts like DEMO that require explicit interaction between research and management and are long-term in nature will require effective empowerment to succeed. Specific legislative direction is a common vehicle for this purpose. Efforts such as DEMO should have: (1) firm legislative or executive authority, (2) financial authorization, (3) a policy framework that allows research and management to collaborate effectively (e.g., that allows transfer of funds), and (4) clearly articulated objectives covering the entire duration of the program (to ensure stability). DEMO has evolved through a piecemeal approach in its legislative authorization. It has received funding on an annual basis, but only through negotiation, and with no assistance in bridging some of the policy elements that make collaboration between research and management difficult. Some of these needs have been partially met through the administrative adoption of a new Memorandum of Understanding by Regional Forester Robert Williams and Pacific Northwest Research Station Director Tom Mills.

2. ***A well-developed, clearly articulated management structure.*** Management models with a clear charter and an effective decision-making process will be most successful. DEMO has been challenged by rather dramatic changes in its management structure, in part due to conflicts involving the Federal Advisory Committee Act (FACA) or, at least the agency's interpretation of FACA. FACA resulted in the removal of key university faculty from direct involvement in decisions about the design or implementation of the study, including some of the people who were responsible for the original congressional direction and funding. Fortunately this did not happen until after the debates about the experimental design had concluded; however, it did mean that subsequent planning and implementation took place without the direct involvement of the instigators. Creation of a Scientific Oversight Committee and a DEMO Coordinating Group were useful contributions to the management structure. The DEMO Coordinating Group has been critical to resolution of issues associated with implementation of the experiment and allocation of resources. Among various possible approaches would be: (1) early development of a more formal structure for decision making and implementation with defined responsibilities, (2) modification of FACA (or its application) to allow continued involvement of key non-agency personnel in design and implementation of the project, and (3) continuity in personnel administering the project.

3. ***An efficient research planning process.*** Large-group science is extremely difficult to conduct. It requires strong centralized leadership.

Leadership in the early planning stages of DEMO was diffuse and uneven, resulting in far too many fundamental design changes. The level of "democracy" involved was nearly fatal. Large-scale, interdisciplinary experiments that address research-management issues will be fraught with many problems—some conceptual, others operational. During the evolution of the DEMO design, conceptual problems included fundamental disagreements about the inclusion of a clearcut treatment, the underlying analytical approach (ANOVA vs. regression), and the nature and extent of post-harvest silvicultural treatments (e.g., weed control, thinning, or other common stand management strategies). Operationally, design and implementation have been challenged by relatively high levels of variation in pre-treatment conditions within study blocks and large differences in stand structure and environment among blocks (Aubry et al. 1999, Halpern et al. 1999); difficulties in meeting all of the requirements of NEPA; and other logistical problems that in many cases reflect the differences in culture between research and resource management entities. We have learned that a clearly designed planning and decision process that identifies and addresses potential conflicts can be used to efficiently work through these types of problems.

4. ***Commitment of lead researchers to the coordination and planning required for success.*** One of the more difficult problems with DEMO has been that key participants have been involved in many activities in addition to DEMO. While most have attended to their disciplinary responsibilities effectively, some have been unable or unwilling to invest the necessary time and effort to ensure clear interdisciplinary communication. On the participant side, involved scientists and managers must make adequate commitments of time, especially to coordination and communication processes. On the agency or contractor side, there needs to be a commitment of adequate multi-year resources. In addition, one or more program coordinators need to be committed exclusively to management of the project.

5. ***Effective collaboration between research and management and among scientists.*** Effective collaboration requires a high level of understanding by researchers of the constraints of management and vice versa (see Abbott et al. 1999). However, basic vocabulary and operating styles differ between research and management, and between federal and academic institutions. Early planning efforts where significant time is devoted to institutional and cultural orientation before any substantive research planning begins will pay dividends. For instance, short-term exchanges of research and management personnel might be possible, or collaboration might be encouraged during short, intensive research sessions or workshops. Recently, the DEMO Coordinating Group has found bi-weekly conference calls and periodic group meetings useful to resolve issues of experimental design and treatment implementation, as well as to facilitate interactions and share philosophies and operational styles. Even with substantial efforts at mutual understanding and communication, it is clear that the goals and constraints of managers and scientists are going to be different and that many decisions will represent compromises.

6. ***A communication program.*** Given the magnitude of the investment and the importance of the issues inherent in large-scale interdisciplinary studies, it is essential that there are mechanisms to share basic information with different constituencies, including Congress, resource managers, and the public. The importance of outreach in obtaining initial as well as continuing support for the project cannot be overemphasized. Possible media include: information brochures, annual (or at least periodic) reporting procedures with publications, symposia, workshops, and special presentations for managers and decision makers. Such efforts must be strongly supported by agency administrators at local, regional, and national levels, however.

The problems posed by large-scale experimentation underscore the need for a strong statistical design and for treatments that offer major, rather than subtle, contrasts. Researchers and managers must recognize the advantages and disadvantages of heterogeneous versus smaller, homogenous treatment areas. Traditional plant science and silviculture emphasize small homogenous plots. While this approach is valuable in many respects, it is inadequate for the study of large-scale ecosystem responses (e.g., responses of wide-ranging vertebrates).

7. ***Sufficient support for data management.*** Identification of critical data management needs, identification of the institutions and individuals

responsible for data management, quality control and archiving, and allocation of financial resources to achieve adequate data management are critical in large-scale ecosystem research. The scale of the task is rarely appreciated and decisions as to the institutions who will undertake the responsibility are generally not an early consideration in the design of such experiments. Furthermore, participants (especially scientists, we think) are traditionally loath to allocate large percentages of a program budget to the data management activity, preferring to spend as much as possible in research—i.e., new data acquisition. In large-scale projects of this type, our experience is that about 20% of the project budget needs to be devoted to the broad category of data management: documentation, metadata preparation, quality control (QA/QC), on-line data provision, long-term archiving, and facilitation of data exchange among collaborating scientists.

Despite the difficulties, large-scale experimentation is necessary to address large-scale problems and challenges in management. There are an increasing number of such enterprises underway. Examples include: (1) the Methods of Alternative Silvicultural Systems (MASS) project on Vancouver Island (Arnott et al. 1995); (2) ecosystem management studies in the Ouachita Mountains, Arkansas (Baker 1994); (3) the Silvicultural Systems Project (SSP) in the State of Victoria, Australia (Squire 1992); and (4) studies on the Black Mountain Experimental Forest, California[2]. Indeed, there is sufficient interest in such projects in Canada that a network—the Forest Ecosystem Research Network of Sites (FERNS)[3]—has been established to facilitate exchange of information among various long-term silvicultural experiments, including organization of a workshop in 1998 on "Long-Term Silvicultural Research Sites: Promoting the Concept—Protecting the Investment."

The MASS project is focused on regeneration, wildlife habitat, and aesthetic concerns in montane forests on the eastern side of Vancouver Island (Arnott et al. 1995). The cost and feasibility of using small patch cuts, green-tree retention, and shelterwood systems are being compared. Harvests were performed in 1993. Each approach has been replicated three times within a single large experimental area; a nearby clearcut and uncut old-growth block provide additional comparisons. The importance of both sufficient funding and committed scientists who are willing to collaborate have been identified in reports about MASS as key factors in making such projects successful. MASS has had substantial financial support from industry and government and has incorporated scientists and students from many different organizations, including several universities.

Several silvicultural experiments are underway in the central region of the United States. One of the most comprehensive of these is a study of alternative harvest cutting practices in mature shortleaf pine *(Pinus echinata)*-hardwood forests on the Ouachita and Ozark National Forests (Baker 1994). This study involves 13 harvesting treatments (11 partial-cutting methods plus unmanaged and clearcut controls) replicated four times, each treatment applied to a 14- to 16-ha stand. Variables under study include microclimate, tree demography, plant community composition, wildlife communities, arthropod and microbial communities, waters and soils, logging and management economics, and scenic quality. Initial harvesting occurred in 1993; thus, to date only preliminary results have been published (Baker 1994). Nevertheless, the interdisciplinary nature of the research team is apparent as is a broad range of participating organizations.

Two related large-scale silvicultural experiments are underway in the Northern Sierra Nevada of California. At the Goosenest Adaptive Management Area, an experiment is directed toward testing alternative techniques to accelerate the development of late-successional forest vegetation in forests which previously had been subject to intensive selection harvest[4]. The harvest treatments involve contrasting emphases on retention of pine or of large trees and, for the latter, an additional comparison with and without use of prescribed fire. The 20 treatment areas (including five untreated controls) are 40 ha in size. A second experiment in northern California at the nearby Black Mountain Experimental Forest is designed to test techniques to maintain and enhance the late-successional characteristics of eastside pine forests that exhibit high levels of natural structural variability. The two harvest treatments involve retention of high and low levels of structural diversity; each treatment is replicated six times with each 100-ha replicate further subdivided into equal areas with and without prescribed burning treatments. True control areas are not a part of the experimental design, although some adjacent ecological reserves provide "qualitative" controls.

One of the earliest of the new generation of silvicultural experiments was the Silvicultural Systems Project (SSP) initiated in 1986 in the Australian State of Victoria (Squire 1992). As originally planned, the SSP and the associated Value Added Utilization System (VAUS) trial were very ambitious in allowing the examination of ecological and economic alternatives across a broad range of forest types. Implementation was much more limited with experimental harvesting confined to three treatments replicated within a single forest type. Funding constraints were the major factor limiting implementation and adequate study of many important topical areas. The deficiencies were sufficient to lead independent reviewers of the project to question whether ". . . the VAUS Program can meet the . . . Government's [informational] needs. . ." (Squire 1992). Eventually the silvicultural experiment was abandoned because of insufficient funding, despite a substantial initial investment.

Experiments such these reflect the growing interest in projects that address large-scale interdisciplinary issues in forest ecosystems; they also demonstrate common approaches and difficulties. True statistical replication is difficult to obtain and, when achieved, typically involves significant tradeoffs in site heterogeneity within treated plots and among replicate sites. Large, multidisciplinary teams with members from a wide array of organizations are typical and substantial communication among individuals must occur if projects are to succeed. Achieving adequate and dependable funding is a very serious challenge in sustaining such studies. Even when they address critical information needs and policy issues, substantial investments may be lost, as in the Australian SSP example.

Conclusion

DEMO was born because of the need to evaluate the scientific basis for some of the newer strategies for forest management in the Pacific Northwest, especially on federal lands. It has brought researchers and managers together in an effort of unprecedented proportion. Through DEMO, both the research and the management community are gaining experience with new approaches to silviculture and resource management. Equally important, DEMO is paving the way to more effective collaboration between research and management. This collaboration lies at the heart of adaptive management, and is essential to the success of ecosystem management.

Acknowledgements

The authors would like to acknowledge the extensive assistance of Kathy Kohm and Charles Halpern in preparation and revision of the manuscript. We would also like to thank several reviewers for their many useful comments: Charles Philpot, Keith Aubry, Bob Devlin, and Charles Peterson. This is a product of the Demonstration of Ecosystem Management Options (DEMO) study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources.

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Endnotes

[1]Memo from John Calhoun, Regional Manager, Olympic Region, WDNR to Larry Mason, Executive Director, Washington Commercial Forest Action Committee, dated June 12, 1992.

[2]For more information on the Black Mountain Experimental Forest, contact the Pacific Southwest Research Station, 2400 Washington Ave., Redding, CA 96001, 916/246-5455.

[3]For more information on FERNS, contact Jim Wood, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, 205/363-0600. Web site: http://www.pfc.cfs.nrcan.gc.ca/practices/fern.htm.

[4]For more information on the Goosenest experiment, contact Kathy Harcken, Pacific Southwest Research Station, 2400 Washington Ave., Redding CA 96001, 916/246-5455.

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Evaluating the Effects of Varying Levels and Patterns of Green-tree Retention: Experimental Design of the DEMO Study

Abstract

In western Oregon and Washington, recent changes in federal forest management policy contained in the Northwest Forest Plan have led to new harvest prescriptions on millions of acres of public lands. For example, on upland sites, standards and guidelines now require that live (green) trees are retained in at least 15% of the area within each harvest unit and recommend that at least 70% of this retention is in patches of moderate to larger size (0.2-1.0 ha or more). These prescriptions for green-tree retention were based on the professional judgement and collective knowledge of many of the biologists who have studied the organisms and ecological processes that characterize these forests, but they have not been rigorously tested nor implemented on a broad geographic scale. Several prescriptions for green-tree retention are being evaluated experimentally by the Demonstration of Ecosystem Management Options (DEMO) study. In this paper, we briefly review recent changes in forest management policy and existing information gaps that led to the establishment of the DEMO study. We then provide an overview of the criteria for site selection, the experimental design and harvest prescriptions, the scope of scientific inquiry, and the collaboration that has occurred between scientists and land managers. These discussions provide the context and experimental framework for the individual research papers that comprise the remainder of this volume.

Introduction

In the 1980s, public concern over the fate of the northern spotted owl (*Strix occidentalis caurina*) and of the old-growth Douglas-fir *(Pseudotsuga menziesii*) forests on which it depends (Gutiérrez and Carey 1985, Thomas et al. 1990) led to unprecedented local and regional interest in natural resource management in the Pacific Northwest. This interest, and the political activism it generated, elevated these issues to national prominence (Ervin 1989, Norse 1990). Lawsuits initiated by environmental groups resulted in injunctions from three separate federal district courts and brought timber sale programs to a standstill on federal lands managed by the USDA Forest Service and USDI Bureau of Land Management (Tuchmann 1995). In April 1993, in response to this 'timber crisis', President Clinton commissioned the Forest Ecosystem Management Assessment Team (FEMAT 1993, see also articles in Vol. 92(4) of the Journal of Forestry) to formulate and assess the consequences of an array of options for managing federal forest lands within the range of the northern spotted owl. This assessment was the first attempt to develop a comprehensive plan for ecosystem management on a broad geographic scale. The resulting management plan came to be known as the Northwest Forest Plan (Tuchmann et al. 1996). The Record of Decision (ROD) and associated standards and guidelines (S & Gs) for the Plan were published in April 1994 (USDA and USDI 1994a) and lawsuits against the Plan were resolved in favor of the government in December 1994.

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Among the changes in forest management policy brought about by the Northwest Forest Plan is a greater emphasis on maintaining the diversity of species, structures, and physical and ecological processes that are important to the functioning of mature, late-successional forest ecosystems. These include microclimates associated with interior-forest conditions, spatial heterogeneity in forest composition and structure, fungi, invertebrates, saprophytic plants, nongame wildlife, snags, down woody debris, and other structural and compositional features generally associated with old-growth forests (Franklin et al. 1981).

This is not the first time that forest management objectives have shifted in response to changing public perceptions or professional judgements. From the 1930s until the mid- to late-1940s, selective cutting of the largest and most vigorous trees was widely applied in old-growth Douglas-fir stands in the Pacific Northwest. Long-term studies revealed, however, that subsequent windthrow mortality was significant and offset increases in residual stand volume for at least 25 yr after harvest (Isaac 1956). Clearcutting replaced selective logging in most areas, and from the 1950s through the late 1980s, regeneration harvests consisted primarily of clearcuts of various sizes staggered in time and space, followed by slash burning and planting. This strategy was designed to meet legal mandates for multiple-use management on public lands while providing high volumes of timber at relatively low cost, dispersion of cumulative watershed effects, access for recreation, and habitat for deer and other game species associated with early successional forests.

Several studies are proposed or underway in the Pacific Northwest region to evaluate the effects of silvicultural prescriptions designed to accelerate the development of late-successional forest characteristics in young, managed stands that have regenerated after clearcutting (e.g., Tappeiner 1992, Harrington and Carey 1997, Carey et al. *in press*). Such experiments are both relevant and necessary. However, because of substantial differences in initial conditions—especially the vegetative and structural legacies typical of mature forests—responses to retention harvest in young, managed forests may be very different from those in mature forests. Mature forests generally have a broader array of structures, species, and functions, whereas managed plantations are often structurally and biologically simpler and the development of late-successional characteristics in these stands may require more intensive silvicultural manipulations. Large-scale harvest studies in mature, late-successional forests are lacking. In the Northwest Forest Plan, these forests are defined as single- and multi-storied stands dominated by conifers > 53 cm dbh (USDA and USDI 1994b; pp. 3&4-26). They comprise 682,300 ha of Matrix lands and Adaptive Management Areas (USDA and USDI 1994b; Table 3&4-8) and, thus, are available for timber harvest under the Northwest Forest Plan. Furthermore, old-growth forests are dynamic and it will not be possible to provide cathedral groves of ancient forests for future generations simply by preserving existing old-growth stands (DeBell and Curtis 1993). Today's mature forests will become the old-growth forests of the future; thus, if societal objectives are to maintain wood production while increasing the extent of forest stands with old-growth characteristics, we must begin to develop methods for managing mature forests for these objectives.

In the early 1990s, several private research institutions and public interest groups in Washington and Oregon sought federal funds for research aimed at addressing these information needs. In response to these lobbying efforts, the Pacific Northwest Region of the USDA Forest Service received Congressional direction in 1993 to establish a large-scale silvicultural experiment (see Franklin et al. 1999). The Region, in cooperation with the Pacific Northwest Research Station, subsequently established the Demonstration of Ecosystem Management Options (DEMO) study, a collaborative research effort with the Washington State Department of Natural Resources, University of Washington, Oregon State University, and University of Oregon to evaluate the ecological, physical, and social effects of retaining live (green) trees in harvest units in western Oregon and Washington. The DEMO study is designed to provide information to aid in the development of harvest strategies that will retain or accelerate the recovery of some of the species and key ecological features found in mature and old-growth forests.

In this paper, we briefly review recent changes in forest management policy and existing information gaps that led to the establishment of the DEMO study. We then provide an overview of the criteria for site selection, the experimental

design and harvest prescriptions, the scope of scientific inquiry, and the collaboration that has occurred between scientists and land managers. These discussions provide the context and experimental framework for the individual research papers that comprise the remainder of this volume. Facilitating the integration of research findings among these disciplines was a guiding principle during development of many aspects of the DEMO study.

Management Needs

Adaptive management, a process by which information gained from monitoring the consequences of management actions is used to refine and improve future management strategies (Bormann et al. 1994), is expected to play an important role in shaping future forest management in the Pacific Northwest. To ensure that management prescriptions provide desired benefits, however, they should also be evaluated experimentally using a rigorous and replicated study design. Information gained through such experimentation, which enables researchers to apply inferential statistics to data collected and to minimize the confounding effects of extraneous sources of variation, will provide reliable and broadly applicable results. Several large-scale silvicultural experiments involving various levels of green-tree retention are underway in British Columbia in forests dominated by Pacific silver fir (*Abies amabilis*) and western hemlock (*Tsuga heterophylla*) (Arnott and Beese 1997, Coates et al. 1997, see also Franklin et al. 1999). However, there is little empirical information available to forest managers in the Douglas-fir region on the ecological responses or social and economic tradeoffs associated with various levels and patterns of green-tree retention (Franklin et al. 1997).

Standards and guidelines in the Northwest Forest Plan specify retaining green trees in at least 15% of the area within each cutting unit and recommend that 70% of this retention is in aggregates of moderate to larger size (0.2-1.0 ha or more), with the remainder dispersed either as single trees or in small clumps < 0.2 ha. In addition, to the extent possible, snags and large decadent trees in harvest units should be preserved in green-tree retention patches (USDA and USDI 1994a). These prescriptions reflect the professional judgements and collective knowledge of many of the biologists who have studied the organisms and ecological processes in these forests. However, the ecological and silvicultural effects of retaining various amounts or configurations of green trees in harvest units have not been quantified (DeBell and Curtis 1993). Aggregated and dispersed retention strategies are each hypothesized to have varying ecological consequences and silvicultural applications. Dispersed retention is believed to be most appropriate where ecological objectives require that certain target structures or conditions be uniformly distributed, such as provision of down woody debris and snags or mitigating microclimatological or hydrological impacts. Aggregated retention, on the other hand, is expected to be more effective in maintaining a broader array of structural elements and ecological conditions. For example, aggregates enable the maintenance of all canopy layers including understory vegetation, as well as snags of various sizes and decay classes, in ways that are not possible with dispersed retention. Intact patches of habitat also serve as refugia for various organisms, which may provide source populations for recolonization of nearby regenerating areas (Franklin et al. 1997).

Because empirical information on the ecological effects of retaining green trees in harvest units in mature stands is extremely limited, the short- and long-term consequences for biodiversity of implementing harvest prescriptions in the Northwest Forest Plan are largely unknown. Green-tree retention in mature forests will produce varying responses depending upon the amount and configuration of retained trees. For example, substantially reducing canopy coverage and dispersing retained trees is expected to accelerate the diameter growth of retained trees, but may have adverse consequences for understory species that have an affinity for late-seral or interior forest conditions (Halpern et al. 1999). Green-tree retention in mature stands will influence understory composition and structure; shape future levels of standing and down coarse woody debris; and affect the diversity, abundance, and distribution of many sensitive plant and animal species. Thus, information on the ecological consequences of green-tree retention in mature forests is needed if we are to effectively manage both young plantations and mature forests.

The DEMO study is expected to provide broadly applicable information on the ecological and silvicultural effects of green-tree retention in mature Douglas-fir forests. Results are expected to

be applicable over a large proportion of public and private lands in western Oregon and Washington. The study focuses on regeneration harvests of mature forests dominated by medium- and large-sized conifers. In addition to the more than 680,000 ha of forest in these size classes in unreserved federal lands in the Pacific Northwest, DEMO results will be applicable to thousands of hectares of younger forest as they mature over the next several decades.

Research Questions

The DEMO study is designed to address the following general questions:

(1) How does the proportion of green trees retained at a site influence various biological, physical, and social values?

(2) Given a particular level of green-tree retention, is the spatial pattern of that retention important? In particular, are the effects of retaining trees in undisturbed patches different from those that result from distributing them evenly throughout the harvested area?

(3) If organisms, processes, and values are affected by the level and/or pattern of green-tree retention in the short term, are the effects maintained over time as stands develop?

(4) Do the effects of different levels or patterns of green-tree retention differ among geographic areas or forest communities?

Experimental Design and Site Selection

The DEMO study consists of a randomized block design involving six treatments representing varying levels and patterns of green-tree retention (Figure 1). Each treatment unit is a relatively homogeneous forest stand of about 13 ha, and is square or slightly rectangular (Figure 2). Treatment units consist of upland forest habitats; large streams or wetlands were avoided.

The six treatments are replicated in eight geographic locations (blocks), four in southwestern Washington and four in southwestern Oregon (Figure 3). Although selected blocks may contain a variety of forest communities, Douglas-fir is the dominant tree species in all blocks (see Table 1 in Halpern et al. 1999); forest ages range from about 70 to 200 yr or more (Table 1). Detailed descriptions of the physiographic environments and management histories for each block are presented in Table 1. Treatments were randomly assigned among six units within each block; the six treatments (Figure 1) are:

(1) *100% retention*—A control unit that provides a baseline for assessing the effects of harvest treatments on ecosystem composition, structure, and function.

(2) *75% aggregated retention*—Three circular 1-ha patches are harvested in a triangular array, removing 25% of the stand area. The pattern and distances between the gaps are consistent among blocks.

(3) *40% dispersed retention*—Dominant and co-dominant trees are retained in an even distribution throughout the treatment unit. The total basal area retained in this treatment varies among blocks, and is determined by the combined basal area (± 5%) in the five 1-ha patches of the corresponding 40% aggregated retention treatment.

(4) *40% aggregated retention*—Five undisturbed 1-ha circular patches are retained in the treatment unit; distances among patches are consistent among blocks (see Figure 2).

(5) *15% dispersed retention*—Dominant and co-dominant trees are retained in an even distribution throughout the treatment unit. The total basal area retained in this treatment varies among blocks, and is determined by the combined basal area (± 5%) in the two 1-ha patches of the corresponding 15% aggregated retention treatment.

(6) *15% aggregated retention*—Two undisturbed 1-ha circular patches are retained in the treatment unit. Each patch is located in a diagonal half of the treatment area; the distance between patches is consistent among blocks.

Responses of forest organisms to these treatments will vary depending on the life history characteristics and spatial requirements of the taxa under consideration, as well as the time since treatments were implemented (see Halpern et al. 1999, Lehmkuhl et al. 1999, Cazares et al. 1999, and Progar et al. 1999 for detailed discussions of predicted responses). In general, however, we predict that the diversity and abundance of species associated with unmanaged mature and old-growth forests (see Ruggiero et al. 1991) will decline with harvest intensity and will be lower in dispersed than in aggregated treatments. We also predict that species closely associated with late-successional forests will be unable to persist in the 15%

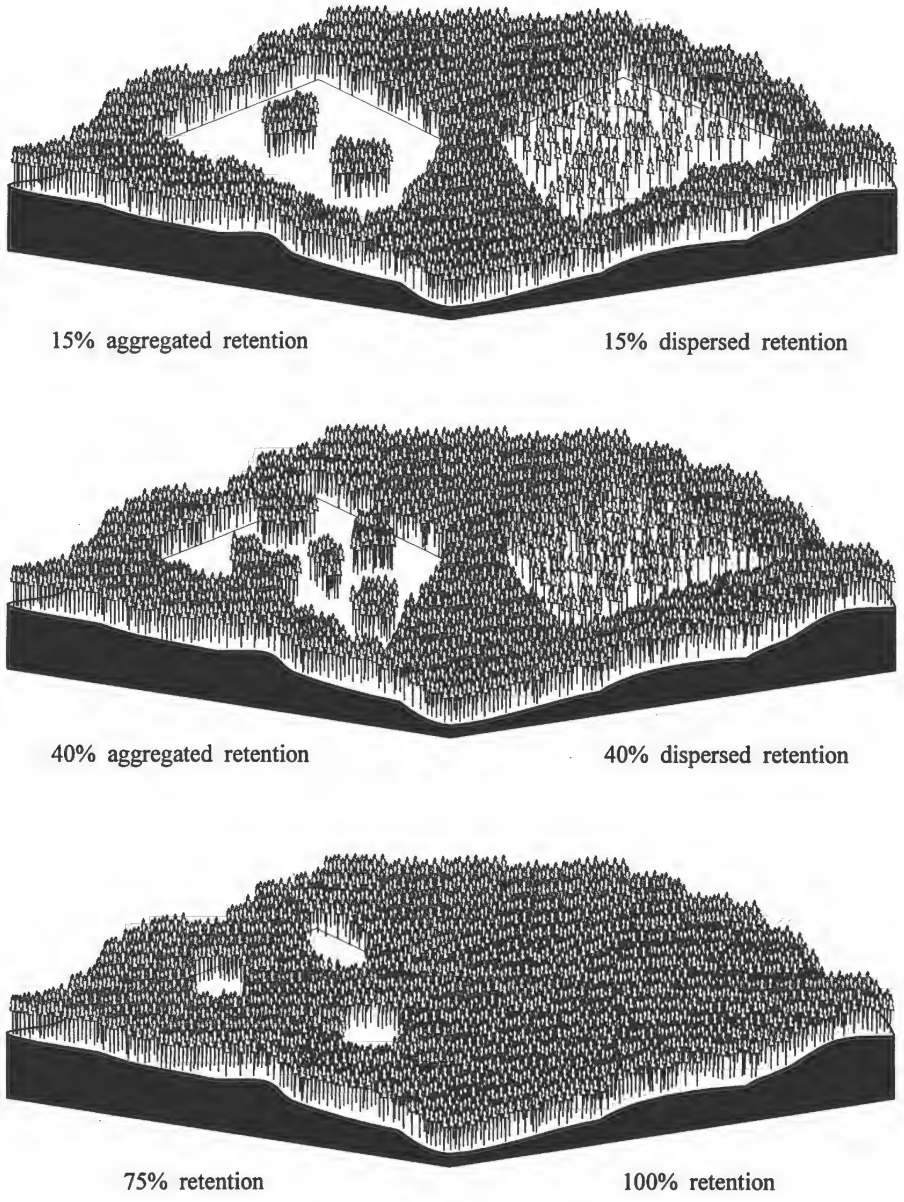

Figure 1. Schematic representation of the six treatments in the DEMO study (figure provided by Ken Bible).

retention treatments, although species with very small spatial requirements may survive in refugia created by the aggregates (see discussion of 'lifeboating' in Franklin et al. 1997).

During the initial planning stages of the experiment, we considered comparing additional levels of retention or varying the sizes of aggregates, but practical constraints precluded these

Figure 2. Aerial view of the 40% aggregated retention treatment at the Paradise Hills block in Washington shortly after harvest (photo courtesy of Jon Nakae).

options (see Franklin et al. 1999). Given the limited availability of suitable areas large enough to effectively study most species of wildlife (especially arboreal rodents) and the funds available for this research, evaluating other levels of retention or sizes and shapes of aggregates was not possible. Site suitability was constrained by many factors, including variation in vegetative structure and composition, roads, management history and allocations, and the presence of streams or wetlands. In many of the blocks, implementation of the treatments required variances from current management requirements, such as those for riparian buffers in the Northwest Forest Plan (USDA and USDI 1994a). Justifications for these variances were reviewed by the interagency Regional Ecosystem Office (REO) and evaluated on a case-by-case basis. The REO concluded "that the review did not identify any unacceptable risks to the objectives of the standards and guidelines that would require modification or cancellation of the project"[1].

It was not possible to select study areas in which the surrounding forests were of uniform stand age, structure, and management history. Thus, we were not able to control the past or future management of surrounding stands; some treatment areas occur within a uniform matrix, while others have a more diverse landscape context. Consequently, landscape-scale influences of surrounding stands on the treatment units may vary. For many response variables, however, such influences are expected to be weak. Lehmkuhl et al. (1991) evaluated the influence of surrounding stands and landscapes on bird, small mammal, and amphibian abundances in unmanaged Douglas-fir stands in southern Washington and found that landscape indices alone were not useful for predicting vertebrate species richness or abundance. For the organisms they studied, physiographic position (especially elevation) and stand structure were much better predictors of abundance patterns than landscape indices. For other wildlife species that may be more strongly influenced by landscape context (e.g., flying squirrels, bats, woodpeckers) the influence of adjacent stands will be considered as covariates in post-hoc analyses of treatment responses.

Methods

Treatment Prescriptions

The experimental prescriptions in DEMO were extremely difficult to apply uniformly among all blocks. This was due partly to differences in geographic location, physical environment, and forest composition and structure, but also to the practical constraints of conducting harvest experiments of this magnitude on public lands (see Abbott et al. 1999). We have addressed these issues in several ways. All prescriptions were applied consistently among the six treatment units within each block. Harvest method, snag and log retention, slash treatment, and planting were similar in all treatment units within each block to ensure that these activities introduced as little extraneous within-block variation as possible. Maintaining complete uniformity in treatments among the eight blocks has proven impractical, but concerted efforts have been made to reduce variability in the implementation of treatments.

The Systematic Sampling Grid

In this study, we use either an 8 x 8 or 7 x 9 sampling grid (to provide flexibility in treatment unit placement) with a 40-m spacing between sample points. The edge of the treatment area extends at least 40 m beyond the outer grid points (Figure 4). The minimum size (13 ha) of the treatment units is based on the area necessary to generate reliable abundance indices for northern flying squirrels (*Glaucomys sabrinus*). Carey et al. (1991) recommended 10 x 10 grids with 40-m spacing

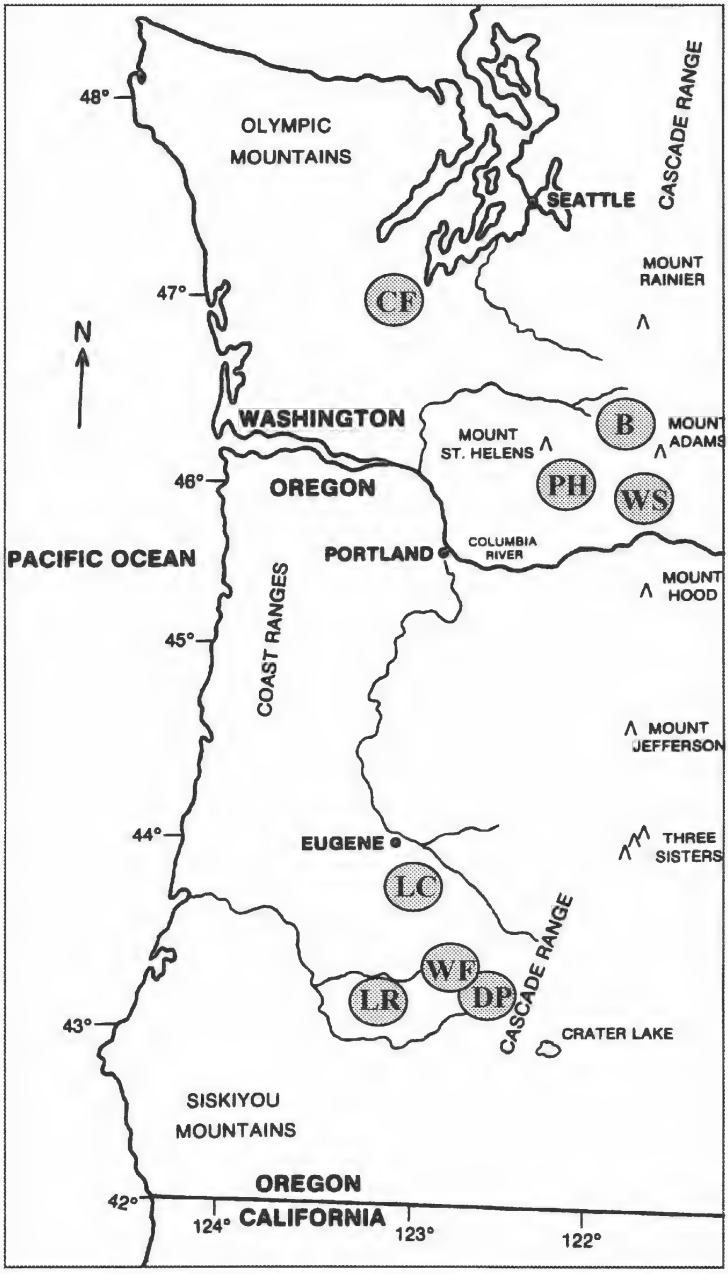

Figure 3. Location of the eight experimental blocks of the DEMO study in Oregon and Washington. Block codes from north to south are: CF = Capitol Forest, B = Butte, PH = Paradise Hills, WS = Little White Salmon, LC = Layng Creek, WF = Watson Falls, LR = Little River, and DP = Dog Prairie.

TABLE 1. Environmental features and stand characteristics of the eight experimental blocks in the DEMO study. Ranges are based on mean values for each of the six treatment units in each block.

Location/Block	Elevation (m)	Slope (degrees)	Aspect	Stand age (yr)	Management history	Riparian zones[1]
Oregon: Umpqua National Forest						
Watson Falls	945-1310	4-7	flat	110-130	salvage logged (1970-1978)	class IV stream (1 unit)
Little River	1220-1400	14-40	varied	200-520[2]	salvage logged (2 units)	class II streams (2 units); class III stream (1 unit); class IV streams (2 units)
Layng Creek	490-790	20-41	SE	60-80	second-growth; thinned (1984-1989)	class III streams (6 units)
Dog Prairie	1460-1710	34-62	SW	165	thinned (1986)	class IV stream (1 unit)
Washington: Gifford Pinchot National Forest						
Butte	975-1280	40-53	E-SE	70-80	none	class III streams (2 units); class IV streams (4 units)
Little White Salmon	825-975	40-66	NW-NE	140-170	none	class III stream (1 unit); class IV streams (5 units)
Paradise Hills	850-1035	9-33	varied	110-140	none	class III streams (3 units); class IV streams (4 units)
Washington: Department of Natural Resources						
Capitol Forest	210-275	28-52	varied	65	second-growth	class III streams (2 units); class IV streams (4 units)

[1]Class II stream = fish-bearing perennial stream; class III stream = non-fish bearing perennial stream; class IV stream = non-fish bearing intermittent stream.

[2]One treatment unit with tree ages of 400-520 yr; remaining units with tree ages of 200-325 yr.

between sample points (16-ha sampling area) for estimating densities of flying squirrels, but indicated that smaller grids (e.g., 7 x 9; 10 ha) were adequate, particularly if the goal was to calculate relative abundance values rather than actual densities (see also Carey et al. 1996).

Study grids were designed so that flying squirrel populations could be included as response variables for several reasons: they are forest obligates associated primarily with mature and old-growth conifer forests, use both canopy and forest-floor habitats, have relatively large home ranges (about 0.8 ha), and are important prey for the northern spotted owl in the DEMO study area (Carey 1991). Thus, the DEMO treatments, which primarily involve manipulating the density and configuration of the forest canopy, are expected to strongly influence flying squirrel populations (see Lehmkuhl et al. 1999). Addressing the needs of spotted owls was a primary objective during the development of the Northwest Forest Plan (USDA and USDI 1994b; pp. 2-72), thus, the response of flying squirrel populations to the DEMO treatments will have important implications for assessing the efficacy of green-tree retention strategies for maintaining or enhancing spotted owl foraging habitat in harvest units.

The permanent grid system (or a subsample thereof) will also be used to sample the responses of various ecosystem components such as vegetation, other wildlife, and ectomycorrhizal fungi. The grid facilitates integration among these studies and ensures that the same environments will be sampled within each stand for the duration of the

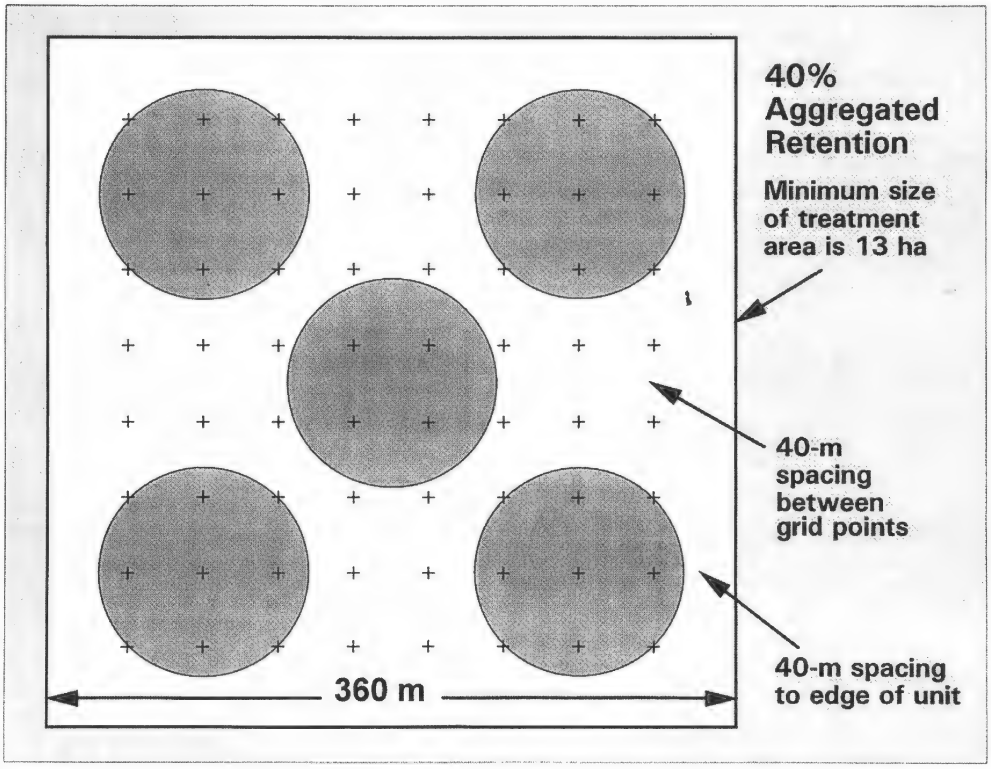
40% Aggregated Retention
Minimum size of treatment area is 13 ha
40-m spacing between grid points
40-m spacing to edge of unit
360 m

Figure 4. Schematic representation of the DEMO experimental grid as configured for an 8 x 8 square grid in a 40% aggregated retention treatment unit.

project. In the three aggregated retention treatments (75, 40, and 15%), in which two contrasting environments will be created (intact forest and clearcuts), the grid will also permit analyses of within-treatment patterns of variability and the contributions of each of these environments to treatment-level responses.

Timber Harvest

Methods for harvesting timber in each block were determined by local forest managers. We recognized that appropriate timber harvest methods would vary in different forest and topographic conditions; thus, it was not practical to use the same harvest method in all blocks. Several constraints were imposed, however: the same method was used in all treatment units within each block, treatment units within a block were harvested in the same year and logging contractors avoided felling trees into retention patches. Four blocks were helicopter logged, two shovel/loader logged, one skyline cable logged, and one block (Capitol Forest, Washington) was logged with a combination of systems due to unusual topographic conditions in one treatment unit.

Snags

During harvest, existing snags that did not pose a safety hazard were retained. To provide snags for future stands and to meet minimum snag requirements specified in the Northwest Forest Plan, contractors left an additional 6.5 dominant or codominant green trees per ha in all harvested areas within each treatment unit for snag creation. These 'snag trees' were retained in addition to the green trees that contribute to the 15, 40, or 75% retention levels in treatments 2 through 6. When possible, trees selected for snag creation

were those that were already decayed or had broken tops. These trees will be killed within one growing season of harvest by removing the crown with a chain saw.

Down Woody Material

Down woody material on site was retained during harvest, but no prescriptions for creating large down woody material were implemented. Green trees that inadvertently fell into unharvested areas of the 75% retention treatment or unharvested patches of the 15% or 40% aggregated retention treatments were removed. When necessary, such trees were limbed prior to removal to minimize disturbance to reserve areas; resulting branches were also removed from the leave areas.

Slash/Fuels Treatment

After harvest, forest managers and researchers evaluated slash loadings to assess potential fire hazards and effects on regeneration and accurate sampling of response variables. If further treatment was necessary, it was accomplished with as little disturbance to the site as possible, using methods determined jointly by forest managers and researchers. Although various methods for fuel-reduction (e.g., yarding tops or hand-piling and burning) were used among blocks, slash treatments were applied consistently among treatment units within each block. Sites having low to moderate amounts of slash were left untreated to provide for soil stability and future nutrient inputs.

Retention of Submerchantable Trees

To the extent possible, trees that were too small in diameter to be merchantable, including advance regeneration (seedlings established naturally under the canopy), were protected in all treatment units.

Riparian Protection

The number of potential study areas that met the size requirements of the study was extremely limited; consequently, it was not possible to avoid small streams or seeps in all treatment units (Table 1). However, to avoid confounding the effects of the primary treatments, undisturbed riparian buffers were not maintained in any of the treatment units.

Reforestation

The Resource Management Plans of the Umpqua and Gifford Pinchot National Forests require minimum stocking densities of 312 trees per ha after 5 years. Evaluation of adequate stocking will be based on planted trees, advance regeneration, and subsequent natural regeneration. Although more than 312 trees per ha may be planted in some blocks to ensure adequate survival, planting density will be set as low as possible to encourage natural regeneration, minimize the need for site preparation, and reduce potential confounding effects on understory vegetation. As with all other prescriptions, planting densities and species composition will be consistent among treatment units within each block and will be determined jointly by forest managers and researchers.

Other Post-harvest Treatments

The use of fertilizers, seeding for erosion control, or herbicides is prohibited on DEMO study sites. Manual release of tree seedlings must be approved by both forest managers and DEMO researchers.

Forest managers have agreed to protect the DEMO study sites from activities that are not part of the planned prescriptions for 10 years after harvest. At that time, managers and researchers are expected to re-evaluate the status of experimental sites and research progress, and assess the need for new study plans, contractual agreements, and additional silvicultural treatments.

Major Areas of Investigation

Given limited time, funding, and human resources, areas of investigation have been restricted to those of highest priority and with the greatest potential for integrative analyses. These include vegetation, wildlife, fungi, invertebrates, hydrology, social perceptions, and harvest costs.

Vegetation

Vegetation studies will examine post-harvest changes in the composition, structure, and diversity of overstory and understory communities both among and within experimental treatments. Variables of interest include the growth, damage, and mortality (including windthrow) of residual trees; recruitment, growth, and mortality of regeneration (natural and planted); changes in species composition of ground-layer bryophytes and lichens, herbs, and shrubs; and the dynamics of snags and down woody debris. Because understory

and overstory measurements are spatially linked, understory patterns can be interpreted relative to initial treatment effects as well as to changes in overstory characteristics. Changes in many of these variables will be used to interpret the responses of organisms and processes under investigation in companion studies (see Halpern et al. 1999 for additional discussion).

Wildlife

Wildlife studies will evaluate patterns of habitat use and provide estimates of relative abundance for diurnal forest birds, arboreal rodents, bats, forest-floor small mammals, and amphibians. Wildlife research will focus primarily on wildlife species with home ranges smaller than the 13-ha treatment areas but, whenever possible, information will be gathered on habitat use by wider ranging mammals and birds. Because animal populations vary annually, 2 yr of pre-treatment data have been collected; additional years of sampling would have been desirable, but were precluded by limitations of both time and funding. Pre-treatment data revealed that flying squirrel populations were too low in several of the blocks to enable meaningful comparisons with post-treatment data. Consequently, flying squirrel populations are only being studied in four of the experimental blocks (two in each state); other wildlife sampling is being conducted in all eight blocks (see Lehmkuhl et al. 1999 for additional discussion).

Fungi

Fungi research will investigate the abundance, community structure, dietary importance for wildlife species, and dynamics of ectomycorrhizal fungi in four of the eight experimental blocks (two in each state). Fungi play a key role in wildlife food webs and influence forest recovery and productivity after disturbance. In addition, the economic importance of edible mushrooms has greatly increased in the Pacific Northwest in recent years; we know little, however, about the effects of green-tree retention harvest on these organisms (see Cazares et al. 1999 for additional discussion).

Invertebrates

Invertebrate studies will address treatment effects on canopy invertebrate diversity, community structure, and population abundances. Canopy invertebrates are important food items for many vertebrate species and are influential in forest ecosystems as both pests and biological control agents. In addition, they affect plant species composition, leaf area, canopy-atmosphere interactions, and nutrient fluxes to the forest floor. Hence, responses of canopy invertebrate communities to forest management practices are particularly important to ecosystem function and forest health (see Progar et al. 1999 for additional discussion).

Hydrology

Hydrologic investigations will focus on snow hydrology, especially rain-on-snow events. Because these winter studies are logistically difficult to implement simultaneously at multiple locations, snow accumulation and melt will be measured at only one experimental block (Watson Falls, Oregon). Supporting meteorological data will be collected so that the physical processes affecting snowmelt and accumulation can be understood for different harvest levels and patterns. Rain-on-snow events are among the most important factors in cumulative watershed impacts, such as flooding, yet little is known about the influence of green-tree retention on this process (see Storck et al. 1999 for additional discussion).

Social Perceptions

Social perceptions of varying approaches to green-tree retention harvest will initially be measured as judgments of acceptability and scenic beauty based on a mail survey of within-stand photographs in several of the harvested blocks. This research will include an evaluation of the influence of demographic characteristics and attitudes toward (1) public forest management practices, (2) the forest products industry, and (3) the potential commodity and non-commodity benefits of the treatments on such perceptions. Once all treatments are implemented, a more intensive survey involving focus groups will be conducted to evaluate public perceptions of the DEMO green-tree retention treatments based on both within-stand and vista views (see Ribe 1999 for additional discussion).

Harvest Costs

Initially, economic studies were proposed as a major component of the DEMO study (Anonymous 1996) but attempts to track logging costs

among treatments were confounded by unanticipated problems in cost accounting. Modifications to the study design to overcome these problems were not possible given practical limitations and funding constraints; consequently, this component of the study was dropped. However, data collected during helicopter logging on the Butte block in Washington will be used to develop a helicopter production and cost simulation model that will be of immediate practical value to forest managers in the region.

Additional Studies

The DEMO harvest treatments and baseline data from each site will provide many short- and long-term opportunities for additional studies that can be accomplished at significantly lower costs than if they were conducted independently. For example, the composition and diversity of arboreal lichen communities have already been studied in several of the Washington blocks as part of a master's thesis (Pipp 1998) and pre-treatment vegetation data provided the ecological context for that study. The DEMO sites and infrastructure are available to other researchers and we welcome additional research partners with extramural funding to establish new, non-destructive studies on the DEMO experimental sites to build upon the baseline research being conducted. Of interest would be studies of treatments effects on microclimate and hydrology, nutrient cycling and decomposition, plant physiology, conifer seed production, and canopy epiphyte and soil invertebrate populations, among others.

Data Collection, Management, and Analysis

An interdisciplinary team of scientists from Oregon State University, University of Oregon, University of Washington, and the Pacific Northwest Research Station are conducting pre- and post-treatment sampling using standard sampling and data collection protocols (see other papers in this volume). Collection of pre-treatment data was completed in 1997 and harvest treatments will be completed in 1999; post-harvest data collection on several blocks began in spring 1998. Although many of the ecological effects will take decades to express themselves, initial post-treatment assessments will be completed within 2-3 yr after harvest. Future assessments, conducted at 5-, 10-, or 20-year intervals, when changes in canopy structure dominate stand-level responses, will be necessary to fully realize the potential benefits of this study and to provide forest managers with comprehensive information on management options for maintaining late-successional conditions in mature forests managed for timber production.

Data management is centralized at Oregon State University's Quantitative Sciences Group, Forest Science Data Bank in Corvallis, Oregon. Comprehensive data entry, verification, and management protocols have been developed, as well as programs to manipulate and reduce the data for subsequent statistical analyses. All data are non-proprietary, but agreements will be developed among participants to govern publication activities. An information management plan has been developed that specifies data management policies, and discusses data input, access, sharing, and security (Anonymous 1996).

No previous studies have been conducted in Douglas-fir forests that involve the experimental treatments, response variables, and geographic scope encompassed by the DEMO study. In addition to standard statistical methods, some innovative biometrical techniques will be applied. Natural variation in forest ecosystems is high and occurs at all spatial scales; consequently, we will partition the variation in ways that separate treatment responses from those associated with environmental variation and other sources of experimental error. Initial analyses will involve the application of standard ANOVA (analysis of variance) tests in accordance with the basic experimental design. Because of the scope and complexity of this study, however, data analyses will not be limited to standard statistical approaches.

Three of the treatments (15% and 40% aggregated retention and 75% retention) will generate two distinct environments within the treatment area—undisturbed forest and clearcut. Response variables for which measurements in the undisturbed forest are not independent of those taken in the clearcuts, such as bird or small mammal abundance values, will be analyzed using treatment-level means. However, for other organisms with more discrete spatial requirements, these treatments will create two distinct responses. Thus, important within-treatment variation may be obscured by only analyzing treatment-level means; for these variables, analyses will also include finer

scale considerations of within-treatment responses (e.g., Halpern et al. 1999).

In addition, there is substantial natural variation both within and among blocks that will influence responses to the treatments; that is, the natural variation present will contribute in specific ways to the effects of the treatments. Sources of variation may include differences in site environment, disturbance history, species composition, or stand structure (e.g., basal area, density, and size structure). Furthermore, in treatments with aggregated retention, the patches contain an intact canopy and have not been disturbed by logging equipment; cut areas in both aggregated and dispersed retention treatments, however, have had their canopies altered and have also been impacted in various ways by the process of removing the trees. Thus initially, the effects of canopy retention will be difficult to separate from the variation in harvest-related disturbance among treatments. However, fine-scale sampling of the types and levels of disturbance (see Halpern et al. 1999) will permit us to evaluate the relative effects of disturbance and retention. Separating these potentially confounding influences may also require the application of more complex analytical approaches, such as longitudinal data analysis (Anonymous 1996).

Integration and Cooperation

The primary vehicles for achieving integration of research activities are the common use of the systematic sampling grid, consistent and uniform implementation of treatments, a centralized and coordinated data management system, and designated scientific and management coordinators working in close collaboration. Many opportunities exist for integration across scientific disciplines including relationships among vegetation, wildlife, fungi, and animal diets; vegetation, birds, bats, and invertebrates; down woody material, snags, and wildlife; hydrology and forest structure; and visual quality and vegetation.

The DEMO study represents a large-scale attempt to conduct comprehensive studies that have direct relevance to ecosystem management. Both planning and implementation have required explicit, ongoing interaction among researchers and managers and, for many, it represents the first opportunity for such collaboration (see Abbott et al. 1999). This process has broadened our collective appreciation of the respective roles and contributions of these two groups in the management of forested ecosystems. These interactions have also presented some challenges, in large part because of legal constraints and differing objectives and approaches among scientists and managers (see Abbott et al. 1999, Franklin et al. 1999). Managers seek to minimize or mitigate potential negative impacts, whereas researchers are concerned with evaluating those impacts in a systematic, unbiased way.

During the design and implementation of the DEMO study, numerous compromises were necessary to resolve conflicting objectives (see Franklin et al. 1999). Research objectives were modified to reduce the number and area of harvest units, and potentially adverse environmental impacts (e.g., those that violate NEPA restrictions) were minimized by avoiding sites that were particularly sensitive to disturbance. Nevertheless, harvest units are larger and silvicultural prescriptions more rigid and restrictive than managers would otherwise implement. In addition, the research requirement for random assignment of treatments contrasts with approaches that would optimize current land management objectives. In most cases, however, managers have been willing to implement rigid treatments and involve the public in ways that differ from current practices (see Abbott et al. 1999).

Scientists and managers will benefit equally from direct involvement in this study. Technical information will be transferred directly to managers, resource specialists, and the public; researchers will gain a new understanding and appreciation of the management process; and fundamental assumptions used to develop green-tree retention standards and guidelines in the Northwest Forest Plan will be tested. The constraints under which resource managers must work are little known to most researchers, and the experiences gained from this study will be useful in designing future studies that contribute to the information needs of those who manage public forests. This sharing of knowledge and experience is central to the DEMO study, and will become more critical as we implement the concepts of adaptive ecosystem management and develop closer working relationships between scientists and land managers. The DEMO study sites will serve as evolving demonstration areas and outdoor laboratories for resource managers,

scientists, educators, and the public for decades to come.

Acknowledgements

Many individuals contributed to the design and implementation of the DEMO study including: Larry Bednar, Gary Clendenen, Robert Curtis, Dean DeBell, Richard Haynes, John Henshaw, John Lehmkuhl, Steve MacDonald, Don Minore, Martin Raphael, and Fred Swanson of the Pacific Northwest Research Station, USDA Forest Service; Rick Abbott, Debbie Anderson, Debbie Couche, Barbara Fontaine, Fred Henchell, Wayne Kleckner, Sue Macmeeken, Jon Nakae, and Ed Tompkins of Region 6, USDA Forest Service; Dean Berg, E. David Ford, Jerry Franklin, and Joel Reynolds of the College of Forest Resources, University of Washington; Logan Norris, John Tappeiner, and David Hibbs of the College of Forestry, Oregon State University; and Richard Bigley, Jeff DeBell, Jeff DeGraan, Jim Hotvedt, Michael Perez-Gibson, John Shumway, and Lenny Young of the Washington State Department of Natural Resources. A special thanks to Bob Williams, Ted Stubblefield, and Don Ostby of the Pacific Northwest Region, USDA Forest Service; Jennifer Belcher of the Washington State Department of Natural Resources; and Tom Mills of the Pacific Northwest Research Station, USDA Forest Service for their significant contributions to establishing this study and ensuring its completion.

This is a product of the Demonstration of Ecosystem Management Options (DEMO) study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources.

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Response of Forest Vegetation to Varying Levels and Patterns of Green-tree Retention: An Overview of a Long-term Experiment

Abstract

Timber harvest with retention of live ("green") trees, snags, and logs is now a standard practice on federal "matrix" lands within the range of the northern spotted owl. Although specific guidelines have been adopted for the levels and spatial configurations of retained structures, neither the ecological assumptions that underlie these recommendations nor the outcomes of these practices have been rigorously tested. The Demonstration of Ecosystem Management Options (DEMO) study examines the responses of forest ecosystems in the Pacific Northwest to varying levels (percentage of basal area) and patterns (dispersed versus aggregated) of green-tree retention. In this paper we describe vegetation studies that form the foundation of this long-term, interdisciplinary experiment. We review the results of retrospective analyses and simulation models which suggest that even minimal levels of retention may have important effects on forest development. We describe the characteristics of the DEMO sites, the experimental design, and the principal variables of interest (stand structure, tree regeneration and growth, and understory composition and diversity). We speculate about the silvicultural and ecological responses of forests to varying levels and patterns of retention and focus in particular on the dynamics of the forest understory. We anticipate strong contrasts among treatments in the establishment of early-seral, open-site species, and in the persistence of shade-tolerant plants associated with older forests or forest-interior environments. Short-term responses are likely to be driven by variation in the distribution and intensity of harvest disturbance. Longer-term trends are expected to reflect the effects of contrasting patterns of canopy retention. We conclude by discussing some of the scientific challenges faced in designing and implementing large-scale, interdisciplinary experiments.

Introduction

Traditionally, management of federal forests in western Oregon and Washington has focused on the production, utilization, and regeneration of timber resources. Until fairly recently (late 1980s), clearcut logging and broadcast burning were standard practices. Clearcut units were dispersed in space and time, logging slash was burned to reduce fire hazard and/or competition from non-crop species, and trees were planted with uniform spacing at high densities. It has become increasingly apparent, however, that these harvest practices do not produce the same complexity of pattern as arises through natural disturbance—a complexity that is thought to underlie the recovery of forest ecosystems following large-scale disturbance (e.g., Franklin et al. 1995, Perry and Amaranthus 1997). For example, historic wildfires in the western Cascade Range were episodic, varying in size, frequency, and intensity with elevation, topography, and local climate (Teensma 1987, Morrison and Swanson 1990, Agee 1993). Even where natural fires were catastrophic, individual trees or groups of trees often survived and large amounts of woody debris remained as logs and snags. It has also become apparent that the structural and compositional attributes that develop through conventional management practices differ markedly from those shaped by natural successional processes (Spies et al. 1988, Hansen et al. 1991, Spies and Franklin 1991, Halpern and Spies 1995, Tappeiner et al. 1997).

Federal forest management policies and practices have changed significantly in the last decade in response to growing concerns that traditional approaches have led to widespread loss and fragmentation of old-growth ecosystems and to attendant declines in biological diversity (FEMAT 1993, Thomas et al. 1993, Tuchmann et al. 1996). A new framework is emerging, characterized by a shift in emphasis from management of a single commodity resource to a broader consideration of ecosystem components and functions. Loosely defined as "ecosystem management," this approach seeks to incorporate ecological knowledge into forest management to sustain biological diversity, as well as timber production (Kessler et al. 1992, Grumbine 1994, Christensen et al. 1996).

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Consequently, forest managers have begun to implement silvicultural prescriptions that are intended to more closely mimic the processes and outcomes of natural disturbance and succession by retaining structural characteristics of the former forest—in particular, large live trees ("green trees"), snags, and logs (Franklin 1989, Hopwood 1991, Franklin et al. 1997).

Green-tree or structural retention is now a standard component of harvest prescriptions for federal "matrix" lands within the range of the northern spotted owl (*Strix occidentalis caurina*). Although specific guidelines have been adopted for the levels and spatial configurations of retained structures (USDA and USDI 1994), neither the ecological assumptions that underlie these recommendations nor the outcomes of these practices have been tested. The Demonstration of Ecosystem Management Options (DEMO) study is among the first in the Pacific Northwest to systematically examine the responses of diverse groups of forest organisms and processes to experimental variation in the amount and pattern of live trees retained through harvest (Aubry et al. 1998). In this paper we provide an overview of vegetation studies that form a foundation of this long-term, interdisciplinary research. Our studies have two fundamental objectives: (1) to elucidate the effects of the level and pattern of retention on key elements of forest structure and composition, and to suggest possible mechanisms for these effects; and (2) to provide information on changes in forest structure and composition necessary to interpret the responses of the organisms and processes under investigation in companion studies (see Aubry et al. 1999 and other papers in this volume). A goal of this paper—indeed a major goal of this entire volume—is to encourage additional research participation in the DEMO study. There are numerous opportunities to take advantage of the current experimental design and the comprehensive set of baseline vegetation data.

We begin with a review of the literature on the responses of forest communities to retention of green trees: the results of previous experiments, retrospective analyses, and modeling efforts have been useful in designing the current work and have stimulated some of the hypotheses we pose. Second, we describe the range of environments, forest types, and disturbance histories represented by the DEMO sites. Third, we provide a brief overview of the experimental design, discuss the primary variables of interest, and outline our long-term sampling approaches. Fourth, we present a series of hypotheses that focus on the responses of forest understory communities to varying levels and patterns of retention. We discuss the ecological bases of our hypotheses and describe the analytical approaches used to test them. We conclude by discussing some of the scientific challenges faced in designing and implementing large-scale, interdisciplinary studies that must balance ecological interests, experimental rigor, and relevance for forest management.

Vegetation Response to Green-tree Retention: A Review of the Literature

The conceptual basis for green-tree retention lies in the strong functional links among forest structure, biological diversity, and ecological process observed in natural forest ecosystems (Franklin et al. 1981, 1987; Harmon et al. 1986; Maser et al. 1988; Schowalter 1989; Ruggiero et al. 1991; Spies and Franklin 1991; North 1993). There is strong circumstantial evidence that the maintenance and/or recovery of forest organisms and processes following disturbance are enhanced by the persistence of remnant forest structures (e.g., Perry et al. 1989, Franklin et al. 1995, Perry and Amaranthus 1997). Franklin et al. (1997) review the history of development, diversity of goals and approaches, and resulting expectations of silvicultural systems that employ structural retention. Emphasizing the maintenance of biological diversity, they attribute an array of ecological functions to retained structures. For example, residual trees may ameliorate extremes in microclimate (Chen et al. 1993, 1995), provide energy subsidies for heterotrophic organisms (Perry 1994), serve as habitat for arboreal species (Berg et al. 1994, Carey and Johnson 1995, Peck and McCune 1997), serve as sources for recolonization of organisms associated with original stand structures (Busing et al. 1995), or enhance connectivity by facilitating movement of organisms within the matrix of managed forest (Franklin et al. 1997).

Retention of green trees should contribute in similar fashion to the persistence and recovery of forest understory communities, yet, to date, few studies have explicitly addressed this question. We are aware of only a single, short-term study that has evaluated the consequences of dispersed retention for forest understory communities. North et al. (1996) found that, 16 mo after

harvest, the species composition of a dispersed retention unit (27 trees/ha) resembled that of an adjacent clearcut to a greater degree than that of an adjacent, intact forest (reflecting abundant establishment of early successional species). However, shade-tolerant forest species were more diverse and abundant in the dispersed unit than in the clearcut, suggesting that forest understory taxa may benefit from the increased shading and/or reduced disturbance afforded by retained trees. Unfortunately, these short-term, unreplicated observations afford only a limited view of the possible effects of green-tree retention.

Studies of understory responses to thinning in younger forests may offer additional insights. It has been found that thinning generally leads to greater plant species diversity (in large part due to the establishment of invasive or exotic species) and to increased plant cover (Witler 1975, Alaback and Herman 1988, Bailey 1996), although the nature of these responses may vary with the vegetation, environment, or intensity of thinning. For example, where thinning leads to increased dominance by clonal shrubs (e.g., Tappeiner et al. 1991, Huffman et al. 1994), there may be a resultant decline in species diversity (Alaback and Herman 1988). There has been little consideration of the effects of thinning on plant species that are associated with late-seral environments or that are sensitive to logging disturbance (but see Bailey [1996]).

Insights into the potential long-term consequences of green-tree retention for understory communities may be aided by retrospective analyses of natural, two-tiered (two-aged) stands. These young-to-mature forests support an emergent canopy of older, scattered residual trees and have been described as the natural analogues of forests that may develop following retention harvest (e.g., Rose and Muir 1996, Peck and McCune 1997, Zenner et al. 1998). Traut (1994) described differences in understory species composition in plots with and without natural, residual trees and attributed these differences, in part, to the effects of residual trees on the density and composition of the regenerating tree layer. Unfortunately, causal mechanisms cannot be deduced through retrospective analysis, nor is it possible to distinguish direct effects (e.g., shading by residual trees) from indirect ones (e.g., species interactions or local variation in disturbance history, initial composition, or other site features). Replicated, pre-treatment measurements in the DEMO study will provide a basis for separating the potential effects of retained trees from initial species composition and other site-level variation.

Considerably more attention has been devoted to the effects of residual trees on forest stand development and tree growth. For example, through analysis of annual growth rings North et al. (1996) observed that for 6 yr after dispersed retention harvest, the basal area increment of retained Douglas-fir (*Pseudotsuga menziesii*) was 15% lower than that in an adjacent, uncut forest. This is not the response typically observed in younger, thinned stands (reviews in Barrett [1980], Bailey [1996], North et al. [1996]); it may reflect a "thinning shock" in which resources are differentially allocated to roots (Oliver and Larson 1990). Long-term measurements of tree growth among replicate DEMO blocks may suggest whether these are local or general phenomena, and whether they represent short-term or more persistent effects.

Retrospective studies of natural, two-tiered stands also provide insights into the long-term effects of dispersed retention on forest development and tree growth. Regional comparisons of 70- to 110-yr-old stands with and without older (>200 yr) residual trees suggest that above a threshold density (ca. 15 trees/ha), residuals can affect the composition of younger cohorts and reduce their basal area growth (Rose and Muir 1996). Negative effects on basal area growth have also been reported from paired-plot studies in western Oregon. Here, however, the strongest effect per unit basal area of residual trees occurred at the lowest levels of residual tree density (5 trees/ha; Zenner et al. 1998) or basal area (5-10 m^2/ha; Acker et al. 1998).

Stand responses to green-tree retention may also include increased mortality due to windthrow of isolated residual trees. Removal of 30-60% of the initial volume of mature and old-growth forests in northwestern British Columbia resulted in rates of windthrow of 0.3 to 8.2% of trees within 2 yr after harvest (Coates 1997). However, mortality can vary markedly from site to site, reflecting variation in the level of retention, initial stand density and composition, stand age, local weather conditions, and landform. For example, among 44 green-tree retention sites in western Oregon, rates of windthrow-related mortality ranged from 0 to nearly 60% (mean of 16%), with the greatest losses observed soon after harvest (Adler [1994]

and Hunter [1995] cited in Franklin et al. [1997]). By comparison, annual rates of mortality in unmanaged mature and old-growth forests of western Oregon and Washington average <1% (Franklin et al. 1987). The randomized block design of the DEMO study will permit separation of treatment effects (level or pattern of retention) on mortality from effects associated with site-specific factors (e.g., topography, soils).

Forest gap and stand-level growth and yield models have also been used to explore the possible effects of varying levels of dispersed retention on forest stand development and wood production. Some of the predictions of these models are intuitive (indeed some are predetermined by growth equations, McKenzie 1994). For example, the degree to which models simulate the development of old-growth stand characteristics (e.g., tree size-class structure) improves with the number of trees retained through harvest (Hansen et al. 1995), and relative to clearcut logging, cumulative basal area and volume growth are reduced when live trees are retained (Birch and Johnson 1992, Hansen et al. 1995). Other simulation results, although less intuitive, are supported by retrospective analyses of natural stands. In particular, reductions in stand basal area growth per residual tree are predicted to be strongest at the lowest levels of retention (5 trees/ha; Hansen et al. 1995). Still other simulation results are quite surprising and seem to contradict empirical observations. For example, under low levels of dispersed retention (as few as 5 trees/ha) and given sufficient time (240 yr), naturally establishing, shade-tolerant species such as western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) can outcompete planted Douglas-fir (Hansen et al. 1995). To what extent the spatial configuration of residual trees may influence stand development has not been examined empirically or through simulation, despite the fact that aggregated retention is now a standard practice on federal matrix lands in the region (USDA and USDI 1994). Comparisons of aggregated and dispersed retention in the DEMO design explicitly test for such effects.

Methods

Study Areas

To establish a broad geographic and ecological base of inference, eight study blocks were selected to represent a diversity of forest types in western Oregon (Umpqua N. F.) and Washington (Gifford Pinchot N. F. and Washington DNR) (see Aubry et al. 1999). Blocks encompass markedly different physical environments, stand ages, and forest structures (Table 1). Sites were chosen to minimize the variation in environment and vegetation among treatment units within each block, within the constraints imposed by current landscape configurations and past management activities (Aubry et al. 1999). To varying degrees this goal was achieved (but see a discussion of this issue in the Challenges section, below).

Across blocks, elevations range from ca. 200-1700 m, slopes vary from gentle to steep, and nearly all aspects are represented (Table 1). Most sites lie within the western hemlock (*Tsuga heterophylla*) forest zone (Franklin and Dyrness 1973). Two blocks, Little White Salmon and Dog Prairie are located in the more easterly grand fir (*Abies grandis*) and white fir (*Abies concolor*) zones, respectively, and a third, Paradise Hills, occupies the colder, wetter, silver fir (*Abies amabilis*) zone. *Pseudotsuga menziesii* dominates all sites but associated tree species vary from block to block (Table 1).

Forest structure varies among blocks, reflecting differences in stand age (e.g., Little River vs. Layng Creek), regeneration and disturbance history, and physical environment (Table 1). Forest understory composition also varies: some blocks have depauperate ground layers (e.g., Dog Prairie) while others support dense herb and shrub communities (e.g., Layng Creek, Little White Salmon). Despite this heterogeneity, many blocks share the same dominant taxa (e.g., vine maple [*Acer circinatum*], Oregongrape [*Berberis nervosa*], salal [*Gaultheria shallon*], and huckleberry [*Vaccinium* spp.]; Table 1). Differences in stand structure and composition among treatment units within each block are generally small compared to differences among blocks (Table 1; but see Challenges section and Table 4).

Sites have had varying histories of recent disturbance (Aubry et al. 1999). For example, Layng Creek and Capitol Forest are second-rotation stands (i.e., clearcut but regenerated naturally) and all four blocks on the Umpqua N. F. have been thinned or salvage logged. In contrast, the three blocks on the Gifford Pinchot N. F. support mature, undisturbed forest.

TABLE 1. General environmental features and pre-harvest structural and compositional characteristics of the eight study blocks. Ranges are based on mean values for each of the six treatment units within each block.

Location/ Block	Elevation (m)	Slope (deg)	Aspect	Stand age (yr)	Tree density (no./ha)[a]	Basal area (m^2/ha)	Douglas-fir site index (m at 50 yr)	Major (minor) overstory species[b]	Major understory species[c]
Oregon: Umpqua National Forest									
Watson Falls	945-1310	4-7	flat	110-130	310-500	36-52	40-43	Psme (Abco, Tshe, Pipo, Pimo)	Abco, Psme, Amal, Libo2, Symo, Bene, Smst
Little River	1220-1400	14-40	varied	200-520[d]	255-473	82-127	29	Psme (Tshe, Abco)	Tshe, Acci, Bene, Oxor, Actr
Layng Creek	490-790	20-41	SE	60-80	227-331	32-46	34-40	Psme (Acma, Cach)	Acci, Cococ, Gash, Bene, Pomu
Dog Prairie	1460-1710	34-62	SW	165	258-475	72-106	30	Psme (Abco, Abmas, Cade)	Abco
Washington: Gifford Pinchot National Forest									
Butte	975-1280	40-53	E-SE	70-80	759-1781	48-65	27-32	Psme (Tshe, Thpl)	Tshe, Thpl, Acci, Vame, Vapa, Bene, Ptaq
Little White Salmon	825-975	40-66	NW-NE	140-170	182-335	61-77	30	Psme (Abgr, Conu)	Conu, Acci, Acgld, Cococ, Actr, Smst, Bene
Paradise Hills	850-1035	9-33	varied	110-140	512-1005	59-87	26-33	Psme (Tshe, Thpl, Abam)	Tshe, Abam, Acci, Vacc, Vame, Vapa, Gash, Xete, Coca
Washington: Department of Natural Resources									
Capitol Forest	210-275	28-52	varied	65	221-562	54-73	37-41	Psme (Tshe, Thpl, Alru)	Acci, Vapa, Pomu, Gash

[a] Trees >5.0 cm dbh.

[b] Tree species codes: Abam = *Abies amabilis*, Abco = *A. concolor*, Abgr = *A. grandis*, Abmas = *A. magnifica* var. *shastensis*, Acma = *Acer macrophyllum*, Alru = *Alnus rubra*, Cach = *Castanopsis chrysophylla*, Cade = *Calocedrus decurrens*, Conu = *Cornus nuttallii*, Pimo = *Pinus monticola*, Pipo = *P. ponderosa*, Psme = *Pseudotsuga menziesii*, Thpl = *Thuja plicata*, Tshe = *Tsuga heterophylla*.

[c] Based on cover; includes understory trees (<5.0 cm dbh). Species codes in addition to those above: Acci = *Acer circinatum*, Acgld = *Acer glabrum* var. *douglasii*, Actr = *Achlys triphylla*, Amal = *Amelanchier alnifolia*, Bene = *Berberis nervosa*, Coca = *Cornus canadensis*, Cococ = *Corylus cornuta* var. *californica*, Gash = *Gaultheria shallon*, Libo2 = *Linnaea borealis*, Oxor = *Oxalis oregana*, Pomu = *Polystichum munitum*, Ptaq = *Pteridium aquilinum*, Smst = *Smilacina stellata*, Symo = *Symphoricarpos mollis*, Vacc = *Vaccinium ovalifolium* / *V. alaskaense*, Vame = *V. membranaceum*, Vapa = *V. parvifolium*, Xete = *Xerophyllum tenax*.

[d] One treatment unit with tree ages of 400-520 yr; the remaining units with tree ages of 200-325 yr.

Experimental and Sampling Designs

Aubry et al. (1999) describe the DEMO experimental design and harvest prescriptions in an introductory paper in this volume. To review, at each of the eight study blocks (replicates), six harvest treatments have been randomly assigned to 13-ha experimental (treatment) units. Treatments differ in the level (percentage of basal area) and/or spatial pattern (dispersed vs. aggregated) of retained trees as follows: (1) 100% retention (control); (2) 75% retention (harvested as three circular, 1-ha gaps—henceforth the "gap" treatment); (3) 40% dispersed retention; (4) 40% aggregated retention (as five, circular 1-ha retention patches); (5) 15% dispersed retention; and (6) 15% aggregated retention (as two, circular 1-ha retention patches) (see Figure 1). By design, these treatments produce distinctly different patterns of variation in stand structure and environment: relatively homogeneous conditions in the control and dispersed retention treatments, and two contrasting conditions (intact forest and harvested area) in the aggregated retention and "gap" treatments. We employ two sampling designs to capture the contrasts and gradients in vegetation response that are expected to arise from these treatments.

Sampling Design for Treatment Effects

The first sampling design, which permits analysis of treatment effects (e.g., Hypotheses 1-3, below), uses a set of permanent vegetation plots arrayed across a grid system at each site (63 or 64 grid points with 40-m spacing, Figure 1). The number and spatial distributions of sample plots vary by treatment, however. In the dispersed retention and control treatments, where stand conditions will be relatively homogenous, 32 plots are placed systematically at alternate grid points (Figure 1a). In the aggregated retention and gap treatments, where we expect two distinct post-harvest environments, plots are placed at all grid points within the aggregates (or gaps), and at a subset of points in the surrounding matrix (yielding 32 or 37 plots per treatment, Figure 1b).

Strong contrasts in harvest treatments will produce marked differences in the composition, size structure, and spatial distribution of overstory trees. We are particularly interested in the effects of these treatments on volume and basal area growth; stem

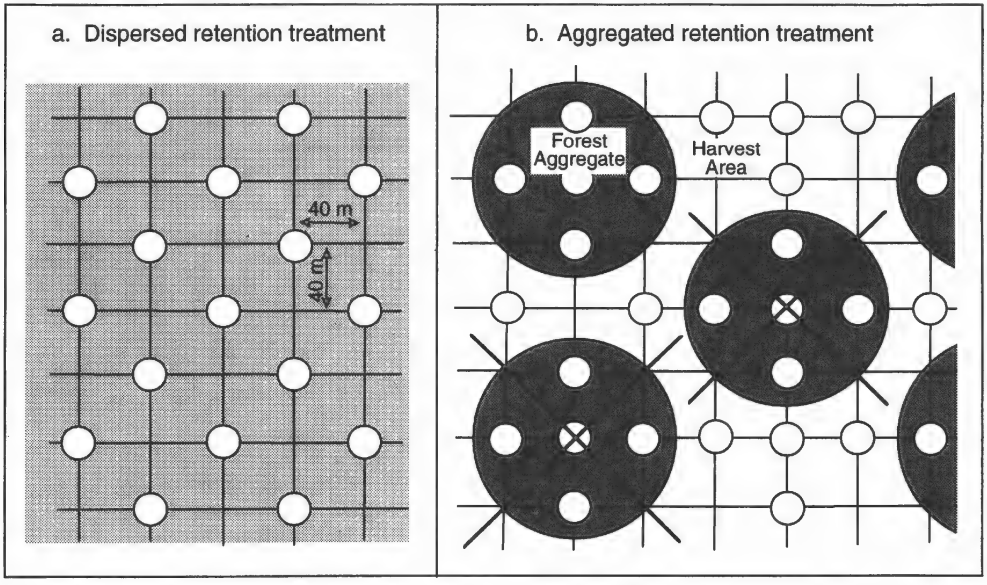

Figure 1. Plot locations (*open circles*) for sampling (**a**) relatively homogeneous conditions in the dispersed retention treatments and (**b**) contrasting conditions in the aggregated retention treatments. Control units are sampled as in (**a**); "gap" (75% retention) units as in (**b**). Spatial gradients within aggregated retention units are sampled using ca. 100 m long transects (dark lines in **b,** see also Figure 2).

TABLE 2. Variables of interest and derived statistics for the two primary sampling approaches (see Methods and Figure 2). X = variable sampled; blank = variable not sampled.

Variable	Treatment-level effects	Within-treatment[a] gradients	Derived statistics
Physical Site Characteristics			
Elevation, aspect, slope	X	X	
Topographic position, slope configuration	X	X	
Ground surface conditions (e.g., mineral soil, stone, litter, log)	X	X	
Coarse woody debris	X		volume and density (by species and decay class)
Post-harvest disturbance (e.g., vegetation damage, soil disturbance)	X	X	
Overstory Vegetation			
Canopy cover	X	X	
Tree diameters (>5 cm dbh)	X		density, basal area, volume, and diameter distributions (by species)
Tree characteristics (e.g., canopy class, vigor, crown ratio, damage)	X		
Tree mortality: physical conditions and causes	X		rates and causes of mortality (by species)
Tree heights: total, canopy depth	X		height and canopy depth distributions (by species)
Snags: diameter, height, decay class	X		density (by species, diameter, decay, and height class)
Understory Vegetation			
Lichens: presence/absence	X		species frequency and diversity
Bryophytes: presence/absence	X	X	species frequency and diversity
Herbs: cover, height	X	X	species frequency, diversity, and height distributions
Tall shrubs: cover, height	X	X	species frequency, diversity, and height distributions
Understory trees			
Seedlings (<10 cm tall): no. stems	X	X	frequency and density (by species)
Saplings (>10 cm tall, <5 cm dbh): cover, no. stems, height class, origin (natural vs. planted)	X	X	frequency, density, size structure, and rates of mortality (by species and size class)

[a]Conducted in the 40% aggregated retention treatments at Butte and Paradise Hills blocks only.

density; diameter, height, and canopy-depth distributions of canopy and sub-canopy trees; rates and causes of mortality; and recruitment and fates of snags (Table 2). A series of nested circular plots (Figure 2a) will be used to sample these overstory responses at 3-5 yr intervals. Permanently tagged trees will be measured for diameter, canopy position, structural attributes, and mortality. Tree height and crown depth will be measured for a subset of stems. Snags will be measured for diameter, height, decay class, and angle of lean.

As with the overstory, the forest understory is likely to respond to strong contrasts in harvest-related disturbance (and resulting canopy conditions) among treatments. We are particularly interested in treatment effects on plant species diversity (richness and evenness); community composition and structure (the proportional representation of different plant groups or 'functional' types); and the establishment, growth, and mortality of regenerating trees (Table 2). We will also consider understory attributes that are known to influence the abundance and distribution of wildlife (e.g., plant cover and vertical stratification, recruitment and dynamics of coarse woody debris) (Table 2). A series of belt transects, intercept lines, and microplots nested within each tree plot will be used to sample

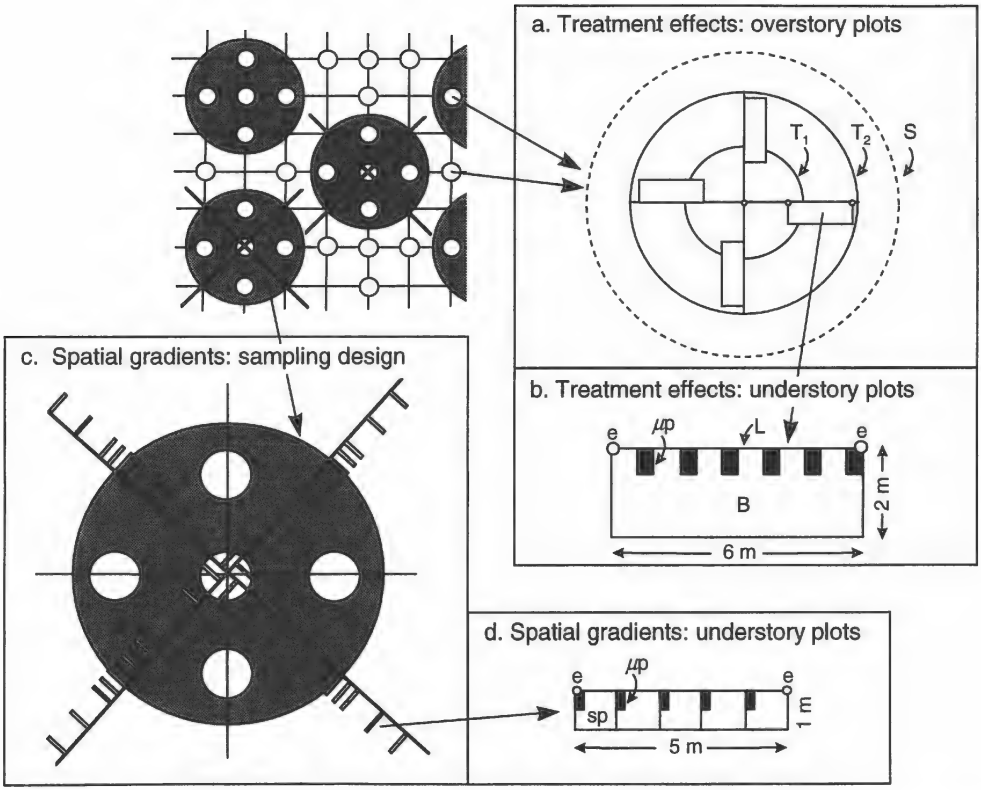

Figure 2. Plot and transect designs for sampling treatment effects (**a, b**) and spatial gradients (**c, d**) within aggregated retention units. For treatment effects, overstory characteristics (**a**) are measured within nested circular plots: 0.01 ha for trees 5.0-14.9 cm dbh (T_1), 0.04 ha for trees >15.0 cm dbh (T_2), and 0.08 ha for snags (S). Understory vegetation (**b**) is sampled with: belt transects (B) for density of saplings (trees >10 cm tall, <5 cm dbh); intercept lines (L) for cover/height of tall shrubs and saplings, disturbance assessments, and volume of coarse woody debris; and microplots (μp, 0.2 x 0.5 m) for ground surface characteristics, presence of bryophytes and macrolichens, cover and height of herbs and low shrubs, and density of tree seedlings (<10 cm tall). Overstory canopy cover is estimated with a spherical densiometer at the end points (e) of each intercept line. For spatial gradients in aggregated retention treatments (**c**), understory vegetation is sampled with 13 bands per transect. Within each band (**d**) are: subplots (sp, 1 x 1 m) for cover/height of all species and densities of tree seedlings/saplings; microplots (μp, 0.2 x 0.5 m) for presence/absence of bryophytes; and end points (e) for overstory canopy cover. See Table 2 for a complete list of variables.

the responses of understory species, changes in ground surface characteristics, and the types and levels of harvest-related disturbance (see Figure 2 caption for details). The nested plot design will also permit direct correlation of overstory and understory characteristics.

Sampling Design for Spatial Gradients Within Aggregated Retention Treatments

A second design will be used to sample fine-scale gradients in understory response within the aggregated retention treatments (e.g., Hypotheses 4-7, below). This approach is limited to the 40% retention treatments at Butte and Paradise Hills. Here our focus is on the extent to which the 1-ha aggregates retain components of the original understory and/or ameliorate microclimatic conditions in the surrounding matrix. Bands of sample plots are arrayed along four orthogonal transects of ca. 100 m in length that span harvested, ecotonal (edge), and intact forest environments (Figure 2c). The perpendicular placement of transects permits examination of the effects of aspect on spatial

gradients in vegetation. Bands are spaced more closely (every 5 m) near the edges (ca. first 15-25 m) of the 1-ha aggregates where we anticipate sharper gradients in vegetation response, and more widely (every 10 m) in the harvested matrix and forest interior (Figure 2c). A series of sub-plots and microplots within each band (Figure 2d) will be used to sample changes in understory composition and structure (Table 2; see Figure 2 caption for details).

Hypotheses, Mechanisms, and Analytical Approaches

It is not possible in this paper to describe the full range of expected ecological or silvicultural responses to varying levels or patterns of green-tree retention. However, to stimulate future discussion and to guide ongoing inquiry and analysis, we have summarized our expectations in a table of predicted, qualitative responses to the six experimental treatments (Table 3). These predictions draw upon the results of empirical studies of natural disturbance and succession, plant-environment relationships, plant life history strategies, and vegetation responses to more conventional methods of silviculture (i.e., clearcut logging, commercial thinning). Others are more speculative and reflect general theory that is untested in these forest ecosystems.

In the following sections, we explore a set of predictions in depth as examples of the types of questions that we have posed in this study. We focus on the response of the forest understory which contains the vast majority of plant species in these forests, and in which we anticipate short-term changes to be most dynamic. Our hypotheses consider three groups of taxa for which we anticipate distinct patterns of response. The first are "forest-interior" species: subordinate forest herbs that are not restricted to, but are found most frequently and with greatest abundance in, forest-interior and late-successional environments (e.g., coral-root [*Corallorhiza* spp.], prince's pine [*Chimaphila umbellata*], rattlesnake-plantain [*Goodyera oblongifolia*], twayblade [*Listera* spp.], pyrola [*Pyrola picta*]; Spies 1991, Halpern and Spies 1995). Many of these herbs are sensitive to disturbances associated with logging and broadcast burning (R5 species of Halpern [1989]; see also Halpern et al. [1992]) and are thought to require long periods of time for populations to recover following large-scale disturbance (Halpern and Spies 1995). The second group consists of "early-seral" or "open-site" species. These include annual, biennial, and perennial herbs (native and exotic) that typically dominate recently disturbed and early successional communities (I1-I4 species of Halpern [1989]; see also Dyrness [1973], Schoonmaker and McKee [1988], Halpern and Franklin [1990]). These taxa are characterized by long-distance seed dispersal, rapid growth rates, and high fecundities. The third group of interest, "forest dominants," are woody and herbaceous species that dominate mature and old-growth forest understories. These taxa are tolerant of disturbance (R3 species of Halpern [1989]; e.g., *Acer circinatum, Berberis nervosa, Gaultheria shallon,* and *Polystichum munitum*) and can occupy a broad range of canopy conditions and seral stages (Spies 1991).

Hypothesized Responses Among Treatments

An underlying premise of green-tree retention is that the survival of organisms associated with forest-interior environments will increase with the proportion of live trees retained through harvest (Franklin et al. 1997). Conversely, invasion of early-successional or open-site species should decline with increased levels of retention. To date, these assumptions have not been tested empirically, nor have the forms of these relationships been articulated (e.g., as linear or non-linear functions, or as threshold responses). There is even greater uncertainty regarding possible differences in response within aggregated and dispersed retention (Franklin et al. 1997). We predict that these groups will respond as follows:

Hypothesis 1.—*The abundance and diversity of forest-interior species will increase with the percentage of green trees retained (Figure 3a).* This prediction rests on two likely outcomes of increasing levels of retention: (1) reduced levels of disturbance to soils and understory vegetation, and (2) greater amounts of shading from retained trees. The results of long-term, successional studies following clearcut logging and burning suggest that both conditions should promote survival of forest-interior species (Halpern 1989, Halpern et al. 1992, Halpern and Spies 1995). In these studies, species extinctions induced by harvest were correlated with the intensity of soil disturbance. In

TABLE 3. Hypothesized short-term (5-10 yr) responses of forest overstory and understory communities to varying levels and patterns of green-tree retention. Responses are relative and represent the *average* condition within each treatment unit (e.g., weighted by area of harvested matrix and forest aggregate), assuming no post-harvest thinning. See Aubry et al. (1999) for details of harvest plans and post-harvest prescriptions.

	Level and Pattern of Retention					
			40%		15%	
Forest Attribute	100%	75%	Dispersed	Aggregated	Dispersed	Aggregated
Overstory Characteristics						
Variability of tree sizes (>5 cm dbh)[a]	high	high	low	moderate	very low	low
Growth release of retained trees	none	none-minor	moderate	minor	moderate	minor
Windthrow-related mortality of retained trees	low	low	low-moderate	low	moderate	low
Variability of snag sizes and decay classes[b]	high	high	low	moderate	low	low-moderate
Understory Characteristics						
Variability of tree sizes (<5 cm dbh)[c]	high	high	low-moderate	moderate	low	low-moderate
Diversity of tree species[d]	low	low	moderate	moderate-high	moderate-high	high
Growth rates of regenerating trees[e]	very low	low	moderate-high	moderate	high	moderate-high
Relative contribution of planted vs. natural regeneration (ratio)[e]	n/a	low	moderate	moderate	high	high
Number of understory vegetation layers[f]	high	high	low	moderate-high	very low	low-moderate
Persistence of forest-interior species (vascular plants)	high	moderate-high	low-moderate	moderate	very low	low
Change in cover of forest understory dominants	none	small decrease	moderate increase	moderate decline	moderate decline	large decline
Recruitment of early-seral, open-site species	very low	low	moderate	moderate-high	high	very high
Persistence of ground-layer bryophytes	high	moderate-high	low	moderate	very low	low-moderate

[a] Retained trees in dispersed retention treatments will be dominants and co-dominants.

[b] All snags will be retained in forest aggregates. In harvested portions of treatments, existing snags will be retained where possible and 6.5 snags/ha will be created from live trees.

[c] Non-merchantable trees will be retained where possible.

[d] Includes early-seral and hardwood species.

[e] Includes planted and natural regeneration. Harvested portions of each unit will be planted with a diversity of species. Planting density (ca. 300-600 trees/ha) and composition will vary by block, but will be consistent among treatments within a block.

[f] Includes all size classes of understory trees (<5 cm dbh).

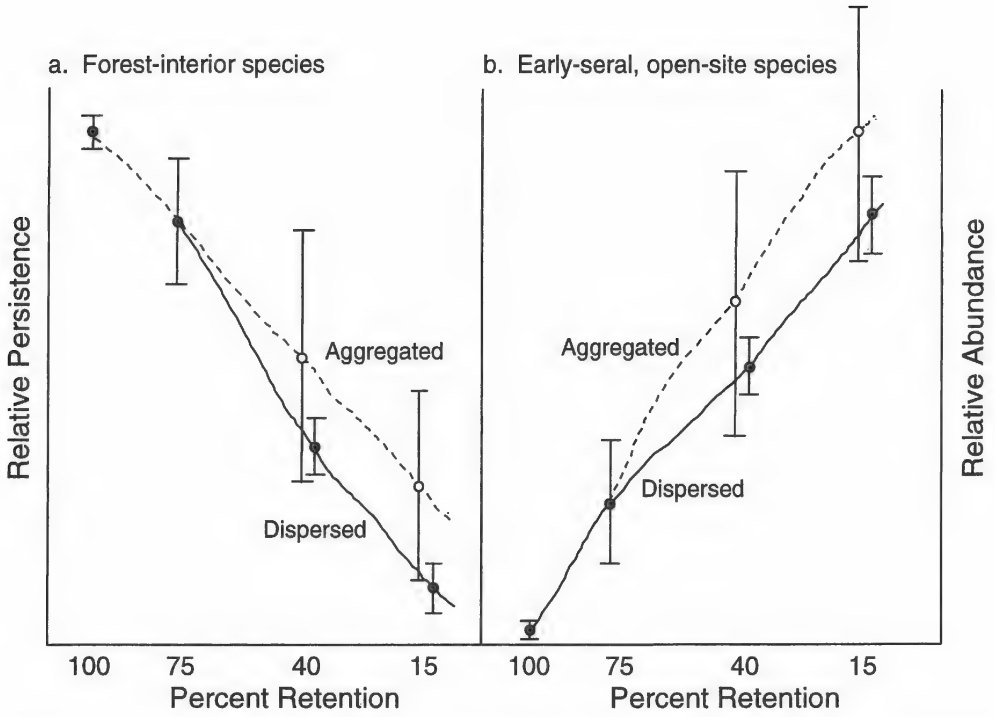

Figure 3. Predicted short-term, qualitative responses (mean and variance) to varying levels and patterns of green-tree retention for two groups of understory taxa: (**a**) forest-interior species and (**b**) early-seral or open-site species.

addition, even where forest soils remained undisturbed, removal of the overstory canopy was sufficient to cause mortality of some sensitive species.

Hypothesis 2.—*The abundance and diversity of early-seral, open-site species will decrease with the percentage of green trees retained (Figure 3b).* This hypothesis has a strong basis in life history theory (Grime 1977, Grace 1990). As light, potential establishment sites, and soil resources become more limiting with greater levels of retention, early-seral species are at a competitive disadvantage. In studies of post-harvest succession, these taxa typically show positive responses to disturbance intensity and negative responses to canopy closure (Dyrness 1973; Halpern 1988, 1989; Schoonmaker and McKee 1988; Halpern and Spies 1995).

Hypothesis 3.—*For both forest-interior and early-seral, open-site species, the mean and the variation in abundance and diversity will be greater in aggregated retention treatments than in dispersed retention treatments (Figure 3).* We assume that in dispersed retention units, uniformly high levels of logging disturbance and associated microclimatic stress will lead to significant loss of forest-interior species and to widespread establishment of early-seral species. In contrast, in aggregated retention units we anticipate spatially distinct patterns of survival and invasion: in harvested portions of these units, survival of forest-interior species will be low and establishment of early-seral species will be high; conversely, in the retention patches, survival of forest-interior species will be high, and establishment of open-sites species will be low.

Analytical Approaches for Hypotheses 1-3.—To test for the effects of treatments on species abundance and diversity, we will use analysis of variance (ANOVA) (or repeated measures ANOVA for long-term effects) coupled with planned comparisons of means (Sokal and Rohlf 1981). Due

TABLE 4. Variation in stand structure and species abundance prior to harvest among the six treatments units at Paradise Hills, Washington. Values are 1996 treatment means. Totals represent the summed cover of all species within a stratum (only selected species are shown).

	Treatment Unit					
			40%		15%	
Forest Attribute	100%	75%	Disp.	Aggr.	Disp.	Aggr.
Overstory Structure						
Tree density (no./ha)	1005	512	877	642	684	732
Basal area (m^2/ha)	70.9	76.1	67.3	58.7	86.7	79.1
Percent Cover of Understory Strata and Selected Species						
Herb stratum (total)	12.7	36.8	19.4	33.5	7.4	6.4
Berberis nervosa	0.3	7.9	1.5	0.2	1.2	0.5
Cornus canadensis	0.9	2.2	1.6	6.7	0.6	1.1
Gaultheria shallon	2.7	9.3	1.2	1.4	0.1	—
Xerophyllum tenax	7.7	10.7	10.2	8.5	2.4	1.7
Tall shrub stratum (total)	6.5	23.4	7.0	28.6	4.0	5.8
Vaccinium membranaceum	0.4	4.6	1.1	10.7	0.2	1.0
V. ovalifolium/V. alaskaense	3.2	7.7	4.0	13.7	2.3	4.4
V. parvifolium	2.5	5.7	1.8	1.9	1.2	0.3
Understory tree stratum (total)	2.5	2.3	8.8	13.6	0.9	3.5
Abies amabilis	1.1	0.2	2.1	10.4	0.6	3.1
Tsuga heterophylla	0.8	1.9	6.0	2.2	0.2	0.2

to the patchy nature of plant species distributions, we have found high levels of variation in frequency, cover, and diversity among pre-harvest treatment units within some blocks (e.g., Table 4). Thus, to improve our ability to detect treatment-level effects we will analyze for *changes* in species frequency, cover, or diversity relative to initial (pre-harvest) conditions. Analysis of covariance (ANCOVA) may be used to test for effects of other potentially important variables (e.g., level of disturbance, cover of coarse woody debris). Species abundance will be measured as frequency of occurrence at varying spatial scales (microplots, transects, and plots) and as mean plot-level cover. Species diversity will be expressed as richness and heterogeneity (Hill 1973) at the same spatial scales. To examine the effects of treatments on the *variability* of responses (*Hypothesis 3*), similar analyses will be conducted using the coefficients of variation of these parameters. Significance levels will be adjusted for multiple comparisons using the sequential Bonferroni method as described by Rice (1989).

Additional correlation and regression analyses will be conducted at smaller spatial scales (e.g., transects or plots) to explore finer-scale relationships with forest canopy cover, shrub-layer development, ground surface conditions, and harvest-related disturbance. These relationships may vary with, or independently of, changes in the level and pattern of retention.

Hypothesized Gradients Within Aggregated Retention Treatments

Aggregates (retention patches) are predicted to serve as refugia for plant species that are sensitive to disturbance or to open-canopy conditions, and as sources of propagules for surrounding harvested areas (e.g., Busing et al. 1995, Halpern and Spies 1995, Franklin et al. 1997). Given the slow rates of dispersal of some understory species (Jules 1997), decades of observation may be required to fully judge the potential of aggregates to serve as sources for recolonization of late-seral species. However, the short-term effectiveness of aggregates as local refugia can be tested by monitoring species' persistence following harvest. The following hypotheses address the extent to which the floristic composition of forest aggregates is maintained through harvest:

Hypothesis 4.—*Within aggregates, species associated with forest-interior or late-seral environments will decrease in abundance and diversity with proximity to the aggregate edge (Figure 4).* This prediction assumes that in fragmented

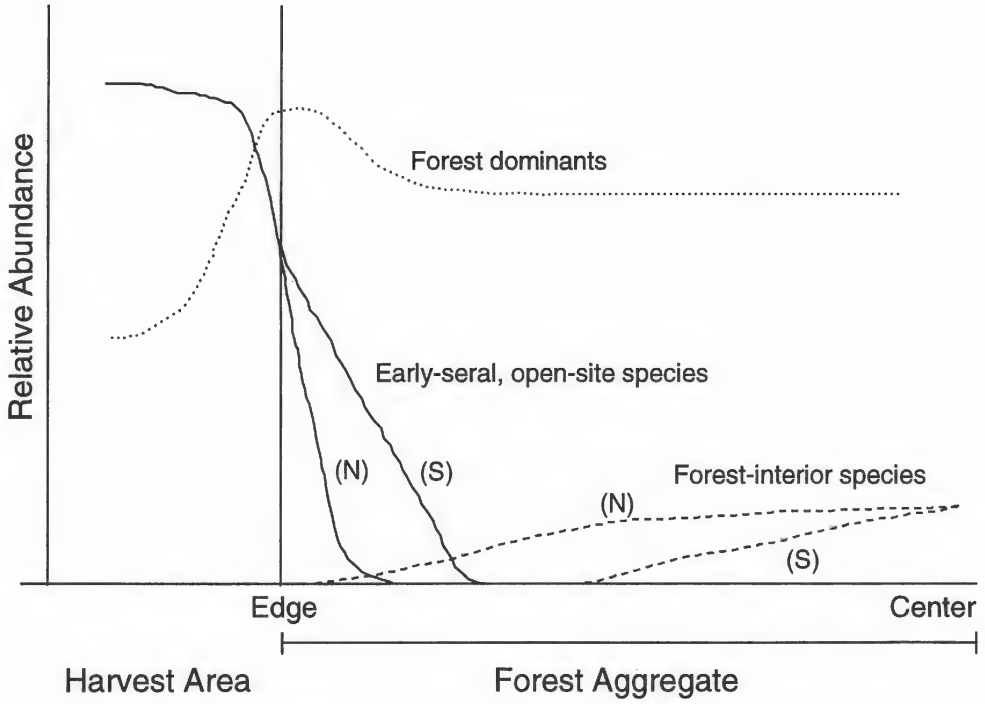

Figure 4. Hypothesized short-term, qualitative responses of three groups of understory taxa as a function of distance from the edge of a 1-ha forest aggregate (radius of ca. 56 m). Responses are expected to differ between north- (N) and south- (S) facing edges.

habitats, the distributions of forest-interior species are shaped by edge effects, manifested as gradients in microclimate, herbivory, or the abundance of competing species. Even if forest structure is retained, forest fragments experience greater variability in air and soil temperature, higher levels of light, greater wind speed, and lower humidity than do larger intact stands (Chen et al. 1992, Matlack 1993). In low-elevation forests of the Pacific Northwest, altered microclimates can extend more than 200 m inward from the forest edge (Chen et al. 1995). (By comparison, the 1-ha aggregates in the current experimental design have radii of ca. 56 m). To what extent understory plants exhibit parallel gradients in response is unclear (Wales 1972; Matlack 1993, 1994a, 1994b; Fraver 1994). Empirical support for the effects of edges on forest understories is scarce in the Pacific Northwest. In the Klamath Mountains of northern California, Frost (1992) found that the abundance of some forest herbs declined for distances of up to 60 m from the forest-clearcut boundary. However, some of the more sensitive herbs observed in these mixed coniferous forests—those with affinities for cooler, moister environments—lie near their southern distributional limits. Our gradient analyses will indicate whether similar patterns are found in the more mesic environments of western Oregon and Washington.

In addition to microclimatic effects, forest edges may also be associated with greater rates of herbivory (Alverson et al. 1988) or regeneration/release of woody plants that can outcompete smaller herbaceous species (Frost 1992) (see Hypothesis 6). Although some forest-interior species may maintain their current distributions, we expect short-term declines in abundance and diversity toward the forest edge. As edge contrasts decline with time (as regenerating stands develop), we expect the gradual recovery of some of these species.

Hypothesis 5.—*Early-seral, open-site species will decline in abundance and diversity with distance into the forest aggregate; gradients in abundance and diversity will be steeper and shorter than those of forest-interior species (Figure 4).* It has been observed in other forest ecosystems that changes in microclimate and local disturbance regime along the forest edge may promote the invasion of exotic or ruderal taxa (Ranney et al. 1981, Laurance 1991, Brothers and Spingarn 1992, Frost 1992). The distances to which early-seral species invade may be more closely linked to the depth of edge-related disturbance than to gradients in microclimate, thus we expect relatively short, steep gradients in response. As the effects of disturbance diminish with time, we expect these gradients in seral species distributions to become less apparent.

Hypothesis 6.—*The dominant forest understory species will show positive responses to the creation of edges, peaking in abundance within a short distance of the forest aggregate-harvested matrix boundary (Figure 4).* Many of our dominant understory taxa (e.g., *Vaccinium* spp., *Gaultheria shallon,* and *Acer circinatum*) possess morphological or physiological traits (e.g., extensive rhizome systems, variable leaf morphology, and/or potential for rapid vegetative spread) that confer resistance to disturbance and enable vigorous expansion once resource conditions improve (Alaback and Herman 1988; Halpern 1988, 1989; Huffman et al. 1994; O'Dea et al. 1995). It is likely that increases in light along the boundaries of newly created forest aggregates will induce rapid lateral and vertical growth of these taxa.

Hypothesis 7.—*Edge effects, as defined by the distances to which early-seral species penetrate or forest-interior species are lost (and by the magnitude of these changes), will be greater where environmental conditions are more stressful (i.e., along south- and west- facing edges as opposed to north- and east-facing edges) (Figure 4).* This prediction is based on the assumption that environmental conditions that inhibit forest-interior species and enhance establishment of open-site species are accentuated along south- and west-facing aspects (Wales 1972, Ranney 1977, Matlack 1993, Chen et al. 1995, Murcia 1995). In the Pacific Northwest, these aspect-related effects may be magnified by greater rates of treefall or canopy damage along south- and west-facing edges due to the strongly directional nature of winter storms.

Analytical Approaches for Hypotheses 4-7.—Analyses of spatial gradients within aggregated retention treatments will be used to elucidate how species abundance (frequency and cover) and diversity vary with distance from the forest-aggregate edge (Hypotheses 4-6, Figure 4). Abundance or diversity measures will be fit to linear or nonlinear regression models (Sokal and Rohlf 1981, Zar 1984). For species that exhibit a significant correlation between abundance and distance from edge, the form of the most appropriate model (e.g., linear, logarithmic, or exponential) may provide insight into the mechanism(s) of decline or advance (e.g., invasion or die-back as isolated individuals or in a wave-front; *sensu* Matlack 1994a). To examine possible aspect-related differences in these effects (Hypothesis 7, Figure 4), we will test for the significance of an aspect term in multiple regressions of abundance on distance and aspect. Multiple regression will also be used in exploratory fashion to test for relationships with other biotic and/or abiotic factors that vary at finer spatial scales and that may influence, or be influenced by, edge-related phenomena (e.g., tree cover, ground surface conditions, local disturbance, or associated vegetation). The sequential Bonferroni method will be used to adjust significance levels for multiple comparisons (Rice 1989).

The 1-ha sized aggregates in the current design are relatively large with respect to the range of prescribed patch sizes (0.2 to >1.0 ha) for green-tree retention units on federal matrix lands (USDA and USDI 1994). However, they are much smaller than are necessary to escape microclimatic effects associated with edges (Chen et al. 1995). Although our studies do not explicitly test for the effects of aggregate size, the results of these gradient analyses may suggest whether smaller aggregates might serve as plant refugia, or whether edge effects are such that larger retention units are necessary to maintain particular species or groups of species.

The Scientific Challenges of Large-scale, Interdisciplinary Experiments

Numerous challenges arise in designing and implementing large-scale, interdisciplinary experiments, particularly when these studies are motivated by concerns over natural resource management or policy. The DEMO experimental design and its component studies represent the products of a long and iterative process in which we have incorporated

diverse ecological interests, a rigorous experimental design, and the needs and concerns of land managers and the public (Abbott et al. 1999, Aubry et al. 1999, Franklin et al. 1999). Many of our decisions represent tradeoffs: they resolve particular problems but in turn may limit statistical power, ecological or silvicultural inference, or harvest efficiency. In this section, we provide several examples of the conceptual and methodological challenges that have shaped our studies.

Sample area and sample size: inherent tradeoffs in interdisciplinary studies. If the spatial scales of sampling in this experiment were not constrained by interdisciplinary linkages, vegetation studies could employ greater replication of smaller-sized treatment units, thus enhancing statistical power. However, vegetation measurements are integral to interpreting faunal responses (Lehmkuhl et al. 1999) which, by necessity, must be examined at larger spatial scales (13 ha). As a consequence, our ability to detect treatment effects for some components of the forest community may be compromised by the relatively small numbers of sample units.

Experimental rigor versus site-specific management approaches. To minimize the potential confounding of post-harvest activities with retention treatments, our silvicultural prescriptions require that site-preparation and tree-planting specifications are consistent among all harvest units within a block (Aubry et al. 1999). However, where experimental units occupy different environments, support different plant communities, or generate different densities of slash, this consistency may lead to a prescription that is less than optimal for silvicultural objectives. Ecological interpretations, as well as the applicability of particular results for managers, must be tempered by these considerations.

Natural variation in vegetation composition and structure. Despite attempts to minimize within-block variability, at some sites topographic configurations, land designations, and past management activities (e.g., adjacent harvest units or roads) precluded the establishment of six, 13-ha experimental units within a forest of homogeneous topography, vegetation, and stand history. Consequently, stand age, forest structure, and species composition vary among experimental units prior to treatment (Table 4). This heterogeneity has implications for interpreting the experimental treatments and resulting ecological responses. For example, because the total basal area retained in forest aggregates dictates the total basal area retained in dispersed units, pre-treatment differences will skew the true proportion of basal area retained.

Variation in vegetation structure and composition prior to treatment (Table 4) must also be considered in interpreting post-harvest responses. To minimize these effects, we will focus on *changes* in abundance/diversity between pre- and post-harvest communities. Nonetheless, where competitive interactions are important determinants of species responses, and where there are large differences in the initial abundance of competitors, effects of treatments may be difficult to detect.

Separating effects of logging disturbance from effects of retention: short-term versus long-term considerations. A primary goal of our research is to elucidate the effects of varying levels and patterns of green-tree retention on forest community development. Although there has been concerted effort to minimize effects of confounding variation (Aubry et al. 1999), operationally, levels of disturbance will change markedly with the proportion of basal area removed and with the pattern in which it is removed. Thus, it is likely that short-term responses of vegetation will reflect differential patterns of logging disturbance as much as, or more than, patterns of retention. Sampling of post-harvest disturbance characteristics will permit an analysis of these effects. As disturbance effects diminish with time, canopy effects may dominate understory responses, although legacies of differential disturbance may continue to shape successional trajectories (Halpern 1988). Thus, green-tree retention strategies incorporate more than variation in the level and spatial arrangement of retained structures—they encompass an array of co-varying patterns and processes. To the extent that we can distinguish disturbance effects from those associated with canopy structures, we may better understand the mechanisms that shape vegetation response and more successfully guide new strategies for forest management.

Acknowledgements

D. Berg and J. Franklin conceived of the original design for a large-scale experiment on green-tree retention in the Pacific Northwest. R. Curtis and

D. Minore contributed to the initial vegetation sampling design. G. Spycher has been instrumental in developing the database management system. The goals and approaches presented in this paper reflect the ideas and suggestion of many individuals: R. Abbott, M. Amaranthus, K. Aubry, L. Bednar, D. Berg, R. Bigley, N. Christensen, D. DeBell, N. Diaz, D. Ford, J. Franklin, M. Hemstrom, A. Horton, D. Neeley, L. Norris, M. Raphael, J. Reynolds, G. Smith, F. Swanson, J. White, and B. Woodard. We thank S. Acker, K. Aubry, P. Burton, D. Luoma, A. Olson, M. Raphael, J. White, and an anonymous reviewer for comments on earlier versions of this manuscript. For their tireless efforts we gratefully acknowledge our field assistants, too numerous to name individually. For logistical support we thank R. Abbott, D. Allaway, D. Anderson, R. Bigley, D. Couche, B. Fontaine, L. Fitzer, F. Henchel, W. Kleckner, S. Macmeeken, J. Nakae, E. Tompkins, J. Walmsley, and J. White.

This is a product of the Demonstration of Ecosystem Management Options (DEMO) study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources.

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An Experiment for Assessing Vertebrate Response to Varying Levels and Patterns of Green-tree Retention

Abstract

The emphasis of forest management in the Pacific Northwest has shifted recently from the production of timber resources to the maintenance or restoration of biological diversity and ecosystem functioning. New standards and guidelines for management emphasize the retention of forest structures (live trees, logs, and snags) to reduce logging impacts, to enrich reestablished stands with important structural features, and to enhance connectivity across forest landscapes. However, little is known about the effects on wildlife of varying the level and spatial distribution of retained structures in forests of western Oregon and Washington. Replicated and controlled experiments within the Demonstration of Ecosystem Management Options (DEMO) study are beginning to quantify the effects of varying the level and spatial aggregation of green-tree retention during forest harvest on a variety of ecosystem components (e.g., vertebrates, invertebrates, vegetation, fungi), as well as snow hydrology and social perceptions of these types of regeneration harvests. Eight replicate blocks of six experimental treatments have been established on the Umpqua National Forest in Oregon, and on the Gifford Pinchot National Forest and Capitol State Forest in Washington. The objectives of the wildlife studies are to quantify patterns of species richness, evenness, and relative abundance of birds, small mammals, bats, and amphibians before and after harvest to examine short-term treatment responses. Pre-treatment sampling has been completed on all sites, harvest treatments are in progress, and post-treatment sampling has begun. In this paper, we present an overview of our hypotheses and methods, and document the occurrence and relative abundance of species prior to harvest of the study blocks. Long-term studies of vertebrate response, habitat associations, and trophic interactions are planned. Results will inform managers on the consequences of alternative forest management strategies.

Introduction

Forest management in the Pacific Northwest during most of the last 50 years has emphasized the production of timber resources. Traditional practices of clearcut logging and artificial regeneration typically produce simplified stand structures that differ from the structural, compositional, and functional complexity of naturally regenerated forests, primarily in the absence of a significant legacy of large live and dead trees and down woody debris (Franklin et al. 1997). The loss of the old-growth legacy and attendant forest complexity has negatively affected the viability of associated species (Harris 1984, Mannan and Meslow 1984, Lehmkuhl and Ruggiero 1991, Ruggiero et al. 1991, FEMAT 1993) and has spurred the development of new forest management strategies for species conservation (e.g., USDA and USDI 1994).

New approaches for managing public forest lands seek to remedy problems associated with past management practices by integrating the maintenance of ecological values with commodity production (DeBell et al. 1997, Kohm and Franklin 1997, Tappeiner et al. 1997). Among these techniques are green-tree or variable retention systems. Retention of green trees in harvested stands has often been translated into the retention of a few

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scattered "wildlife" trees, with little apparent benefit to wildlife (McComb et al. 1993b). More sophisticated retention techniques that vary the level and spatial pattern of retained trees have been proposed to mimic the effects of natural forest disturbance, in particular the retention of large structural elements including live trees, snags, and down wood (FEMAT 1993, Franklin et al. 1997). The objectives of these techniques are to maintain ecosystem structure and function, enrich reestablished stands with structural features that would otherwise be absent, and enhance connectivity across the landscape (Franklin et al. 1997).

Presumably, vertebrate species that persisted within disturbance regimes of the pre-European settlement period may be expected to persist in managed forests if those regimes are mimicked. However, it is unclear how species will respond to our attempts to mimic natural disturbance regimes, as there are few data on the relationships between the levels and spatial patterns of green-tree retention and the short-term persistence or the long-term recolonization of species in harvested stands (McComb et al. 1993a, Chambers 1996, Hansen and Hounihan 1996, Franklin et al. 1997). Retrospective research has focused on species found in unmanaged late-seral and younger forests (e.g., Raphael 1988, Ruggiero et al. 1991, Rosenberg and Anthony 1993, McGarigal and McComb 1995, Gomez and Anthony 1996, Hagar et al. 1996), recent clearcuts (Medin 1986), or stands with evenly-distributed partial retention of green trees (Vega 1993, Hansen et al. 1995, Hansen and Hounihan 1996). Retaining more green trees might maintain components of stand structure or function that will allow some species to persist in harvested areas, but may result in poorer persistence of other species (Hansen et al. 1995, Hansen and Hounihan 1996, Chambers et al. *in press*). Retaining trees in undisturbed refugial patches likewise might result in smaller initial impacts or faster long-term recovery, depending on the life history and population structure of the species. Although the results of relevant experimental studies with pre- and post-treatment data are beginning to emerge (e.g., Chambers et al. *in press*), no studies have been published that examine the effects on vertebrate communities of simultaneously varying both the level and spatial pattern of green-tree retention (Franklin et al. 1997).

As a component of the Demonstration of Ecosystem Management Options (DEMO) study (Aubry et al. 1999), we have been studying responses of forest vertebrate species to experimentally manipulated levels (percentage of basal area) and patterns (dispersed vs. aggregated) of green-tree retention. Our primary goals are to: (1) quantify short-term changes in community composition and abundance of birds, small mammals, bats, and amphibians; (2) identify the vegetation and other habitat attributes associated with observed changes in species occurrence and abundance; and (3) quantify functional trophic relationships (e.g., fungivory) of select species groups.

In this paper we provide an overview of our study area, describe our experimental and sampling designs, briefly review the ecology and habitat relationships of vertebrate groups targeted for study, describe hypothetical short-term (5-10 yr) responses of vertebrates to treatments and the analytical techniques to test these hypotheses, briefly summarize pre-treatment results, and describe the challenges and limitations of implementing an experimental study of this scope on vertebrates. This paper does not contain a detailed analysis of pre-treatment data. Hypothetical responses of vertebrates to the retention treatments are based on current knowledge of species' ecologies and the hypothesized responses of habitat elements to these treatments as described by Halpern et al. (1999). Aubry et al. (1999) provide detailed descriptions of overall project goals, experimental design and harvest treatments, and the full scope of DEMO research (vegetation, fungi, invertebrates, social perceptions, snow hydrology).

Methods

Study Area

Study sites occur in Douglas-fir (*Pseudotsuga menziesii*) dominated forests on the Umpqua National Forest in western Oregon, and on the Gifford Pinchot National Forest and Capitol State Forest in western Washington (see Aubry et al. 1999). The eight study blocks (four in each state) provide a broad geographical and ecological scope of inference (Aubry et al. 1999). Within each block, six study units were selected from the same or adjacent watersheds to reduce differences in physiographic and stand characteristics, and to reduce differences resulting from past management. In contrast, blocks vary widely in biophysical setting and past management. Variation within and

among blocks is accounted for in the sampling design and analytical techniques (see below).

Among the blocks, study sites range from 200-1700 m in elevation, slopes vary from steep to gentle, and nearly all aspects are represented. Stands encompass a variety of disturbance histories, ages, and successional stages, but all have developed beyond the stem-exclusion stage of forest development (*sensu* Oliver and Larson 1990). All stands on the Umpqua National Forest have been thinned or salvaged to some degree, whereas those on the Gifford Pinchot National Forest are all natural unmanaged forests. Two blocks (Layng Creek, Oregon and Capitol State Forest, Washington) are second growth as a result of previous harvest. Forest understories are compositionally diverse, but many blocks share the same dominant herbaceous and woody species. Halpern et al. (1999) provide detailed site descriptions and an overview of the variation among blocks.

Our results should be applicable to portions of the western Cascade and Coast Ranges with similar biophysical conditions and species distributions. Many, but not all, of the vertebrate species of interest occur throughout both regions. Where biogeographic variation in species distributions and responses to treatments may occur (e.g., Carey and Johnson 1995), the block design of the experiment will help to control for some regional differences in treatment effects.

Experimental Design

A randomized block design allows us to control for biophysical differences across the regional study area. At each of eight study blocks (replicates) five harvest treatments and a control were randomly assigned to 13-ha treatment units. After extensive survey of candidate stands across the potential study area, 13 ha proved to be the maximum stand size that could accommodate the minimum sampling grid (described below) and provide for homogenous within-stand biophysical conditions. Treatments vary in the level of retention of live trees (15-100% basal area) and in the pattern of retention (trees uniformly dispersed vs. aggregated). The six treatments are: 100% retention (control); 75% aggregated retention (trees harvested in three circular, 1-ha gaps); 40% dispersed retention throughout the stand; 40% aggregated retention (as five undisturbed, circular, 1-ha patches); 15% dispersed retention; and 15% aggregated retention (as two undisturbed, circular, 1-ha patches). All snags will be retained in forest aggregates. In harvested portions of treatment units, existing snags will be retained where possible, and 6.5 snags/ha will be created from live trees (see Aubry et al. [1999] for details).

Sampling Design and Analytical Methods

Sampling for vertebrates and vegetation within each treatment unit occurred on a permanently marked 8 x 8 or 7 x 9 grid, depending on the shape of the stand, with 40-m spacing between grid points and a 40-m buffer to the edge of the treatment unit. This grid configuration was chosen to conform to sampling methods for arboreal rodents, which require the largest sampling area among all species studied, and to allow for systematic sampling of treatments. Carey et al. (1991) recommend 10 x 10 grids with 40-m spacing (16 ha) to estimate the density of northern flying squirrels (*Glaucomys sabrinus*), but indicate that smaller grids (e.g., 8 x 8 or 7 x 9, [13 ha]) are adequate if the goal is to calculate relative abundance indices rather than density (see also Carey et al. [1996]). Because larger grids could not be accommodated given the sizes of intact stands, we accepted the smaller grid (see Abbott et al. [1999], Aubry et al. [1999] for additional details).

Field methods were designed to index habitat use by numbers of detections or individuals captured. We assume that use will be strongly correlated with changes in abundance for most species of interest. For some species with large ranges of movement relative to the area of treatment units (e.g., bats and some birds), use may not be closely tied to changes in abundance. Thus, the most ecologically meaningful information will be gained from species that occur at moderate to high densities and that exhibit local patterns of movement relative to the size of treatment units.

Data were collected for 2 yr prior to treatment to quantify species occurrences and relative abundances. Comparison of pre- with post-treatment data in testing treatment responses will allow us to control for spatial variation in vertebrate occurrence and abundance among treatment units within blocks. Comparison of data between treatment and control units will control for temporal variation. Although comparisons of pre- and post-treatment data from manipulated and control stands enable us to separate annual variation in species

abundances from the effects of harvest treatments, an understanding of long-term (> 5 yr) responses will require repeated measurements over longer time frames.

We analyzed the power of the experimental design to detect treatment effects on a subset of bird and small mammal species. We chose a focal species (northern flying squirrel), four common and one wide-ranging bird species, and one moderately abundant terrestrial small mammal species that we knew to be well sampled and could be anticipated to be either greatly or minimally affected by treatments. We used pre-treatment data to estimate mean and variance of captures. Treatment response was hypothesized to be at least a 40% (birds) or 50% (small mammals) reduction in captures between the control and one treatment—the 40% dispersed retention treatment—based on the interactions of individual species life histories, habitat relationships, and the level of canopy removal. Nearly all treatment effects are expected to result in greater declines; thus, the test understates the expected magnitude and frequency of treatment effects and gives conservative power estimates.

Treatment effects on individual species abundances (for species meeting minimum criteria for occurrence or abundance in treatment units) and on community attributes of species richness and evenness will be tested as the difference between pre- and post-treatment values among treatment and control units using randomized block analysis of variance (ANOVA) (Skalski and Robson 1992) or nonparametric analogs. Repeated-measures ANOVA will be used to test for long-term treatment effects. Similarity in faunal associations among and within treatments will be examined by clustering or ordination techniques. Relationships between vegetation or other habitat attributes (e.g., volume of woody debris) and species presence or abundance will be examined across all replicates primarily by regression analysis.

Hypotheses, Methods, and Preliminary Results

Birds

Review

Some bird populations are declining in the Pacific Northwest (Sharp 1990, 1992), in part as a result of timber harvesting that shifts tree age-class distributions from old to young and alters natural disturbance regimes (Franklin and Forman 1987, Spies and Franklin 1989, FEMAT 1993). There are concerns for cavity-nesting birds (Morrison et al. 1986, Chambers et al. 1997), neotropical migrants (Hagan and Johnston 1992, Martin and Finch 1995), the northern spotted owl (*Strix occidentalis caurina*) (Forsman et al. 1996), and marbled murrelet (*Brachyramphus marmoratus*) (Carter and Morrison 1992, Nelson and Sealy 1995, Ralph et al. 1995) that have fueled public debate over forest management in the Pacific Northwest.

Significant research has been devoted to bird populations in natural, unmanaged Douglas-fir forests of western Washington and Oregon (Carey et al. 1991b, Gilbert and Allwine 1991a, Huff et al. 1991, Manuwal 1991), and there have been some retrospective studies of birds in managed forests of the region (Artman 1990, McGarigal and McComb 1992, Hansen et al. 1995, Hagar et al. 1996, Hansen and Hounihan 1996). However, replicated manipulations that include pre- and post-harvest sampling (e.g., Bosakowski 1997, Chambers and McComb 1997, Chambers et al. *in press*) have been limited in size and scope.

Bird species associated with mid- to late-successional forests that use large trees for foraging or as nest sites (Brown 1985) typically decline in response to harvest (Franzreb 1977, Keller and Anderson 1992, Chambers 1996, Hansen and Hounihan 1996), although intensity of harvest affects responses differently. Compared with clearcutting, 25% retention of green-tree basal area offers benefits (foraging and nesting habitat) to some of the species associated with old-growth forests (Chambers 1996, Chambers et al. *in press*).

Neither Chambers (1996) nor Vega (1993) detected a significant change in bird species richness among retention-treatment, late-successional forest, and clearcut stands ≥8 ha in area, although the composition of the bird community changed after harvest. However, retention stands provided breeding habitat both for birds associated with early seral stages and for some species associated with late-successional forest. The retention of large trees apparently provided foraging substrates and in some cases breeding sites for some species associated with old-growth forest. However, less intensive harvesting (approximately 30% reduction in wood volume) resulted in decline or loss of fewer bird species associated with late-

successional forests (Medin and Booth 1989, Chambers 1996, Chambers et al. *in press*). Thus, a variety of stand treatments may be necessary to maintain habitat for different species.

Hypotheses

Hypothesis 1—*Abundance of canopy-dwelling birds will decline with decreasing levels of tree retention; aggregation of retention will reduce this effect (Table 1).* Species whose primary habitat is closed-canopy forest, such as hermit/Townsend's warbler (*Dendroica occidentalis/D. townsendi*) and the golden-crowned kinglet (*Regulus satrapa*), likely will decline in abundance with the loss of canopy habitat. Aggregation of patches will allow for some persistence in treatment units.

Hypothesis 2—*Abundance of birds associated with understory vegetation will decline with decreasing levels of tree retention in the short term (<5 yr); abundances will increase in the longer term. Aggregation of retention will ameliorate the effects of decreasing retention (Table 1).* Some vegetation layers, understory shrubs in particular, are predicted to decline in the short-term after harvest (Halpern et al. 1999), but will recover or be replaced by other understory species over long periods of time (>5 yr).

Hypothesis 3—*Primary and secondary cavity-nesting birds will decline with decreasing levels of tree retention and by dispersing the pattern of retention (Table 1).* Increased levels of harvest will result in marked reductions in snags in treatment units with ≤40% retention (Halpern et al. 1999). Old decayed snags, which are valuable for some cavity-nesting birds (northern flicker [*Colaptes auratus*], red-breasted nuthatch [*Sitta canadensis*]), will be lost in treated areas, and creation of replacement snags from sound trees (see Aubry et al. 1999) will have little effect in the short-term. Aggregation of retained trees in undisturbed refugia will likely ameliorate the effect of declining retention on cavity-nesters that use open canopy habitat (e.g., chestnut-backed chickadees [*Parus rufescens*]).

Methods

Bird community composition, species richness, and relative abundance were estimated in each stand from four point-count stations using the modified variable circular plot method described by Reynolds et al. (1980). Spot mapping was conducted during point counts, following procedures by Ralph et al. (1993), to examine locations of territories of selected species (Table 2) relative to canopy and forest floor characteristics before and after harvest.

Bird surveys began in late April and ended by early- to mid-July. Each treatment unit was visited six times during the breeding season. Surveys were evenly spaced throughout the breeding season to capture variation in breeding phenology among bird species. Abundance was expressed as a detection rate (mean number of birds detected within 75 m per visit) to facilitate comparison of species abundance among stands. Count stations were at least 160 m apart, thus 75 m was chosen as a conservative maximum detection distance to avoid recounting individual birds. We combined detections of hermit warblers and Townsend's warblers because of extensive hybridization between the two species (Rohwer and Wood 1998). We later will assess habitat quality and verify breeding status of all birds by using a reproductive index (Vickery et al. 1992) to determine whether species are nesting in the study stands.

Power analyses for four common species showed adequate power in the point-count sampling design to detect changes in detection rates of hermit/Townsend's warblers (0.99), golden-crowned kinglets (0.99), dark-eyed juncos (*Junco hyemalis*) (0.97), and brown creepers (*Certhia americana*) (0.96). Power was inadequate (0.52) for the less common and wider-ranging gray jay (*Perisoreus canadensis*).

Summary of Pre-treatment Results

Using the point-count data, we selected those species for which some analyses might be possible in one or more sites. Criteria for selection were species that were observed within 75 m of the observer and species that had 30 or more detections in a block in either of the two pre-treatment sampling sessions. A threshold of 30 detections was evident in the frequency distribution of pre-treatment detections and was thus used to separate common from uncommon species. In Washington, 15 of 51 species detected fit the criteria for analyses and in Oregon, 12 of 70 species (Table 2). There should be adequate power to

TABLE 1. Predicted short-term (5-10 yr) responses of vertebrate species to green-tree retention treatments in the Demonstration of Ecosystem Management Options study. Response is the predicted change in abundance from measured pre-treatment values: 0 = no detectable effect, - = decline in abundance, + = increase in abundance. Single, double, or triple entries indicate hypothesized responses that are weak, moderate, or strong, respectively. Double entries separated by a comma indicate the range of uncertainty in predicted response.

	Level and Pattern of Retention				
Species	75%	40% Dispersed	40% Aggregated	15% Dispersed	15% Aggregated
Birds					
Hammond's flycatcher	+	+	0	-	--
Pacific-slope flycatcher	-	--	--	---	---
Chestnut-backed chickadee	-	--	-	--	-
Red-breasted nuthatch	-	--	-	---	--
Brown creeper	-	-	-	---	--
Winter wren	-	--	--	--, ---	--, ---
Hermit thrush	0	--	-	---	-
Swainson's thrush	0, -	0, -	0, -	-	-
Varied thrush	-	--	-	---	--
Golden-crowned kinglet	-	--	-	---	--
Black-throated gray warbler	0	0	0	-	0, -
Hermit/Townsend's warbler	-	--	-	---	--
MacGillivray's warbler	+	+	+	++	++
Wilson's warbler	0	-	-	-, --	-, --
Dark-eyed junco	0	0	0	0	0
Mammals					
Montane shrew[1]	0	-, 0	-, 0	-, 0	-, 0
Fog shrew[1]	0	0	0	0	0
Trowbridge's shrew[2]	0, -	-, --	-, --	--, ---	-, ---
Vagrant shrew[1]	0, +	+	+	++	++
Shrew-mole[2]	0, -	--	-, --	---	--, ---
Coast mole[2]	0	-	-	-	-
Siskiyou chipmunk (OR)[3]	0	0	0	-	-
Townsend's chipmunk[3]	0	0	0	-	-
Douglas' squirrel[3]	0	--	-, --	---	--, ---
Northern flying squirrel[3]	-	--	-, --	---	--, ---
Deer mouse[1]	0, +	+, ++	+, ++	+, +++	+, +++
Forest deer mouse (WA)[2]	0	-	-	-, --	-, --
Bushy-tailed woodrat[3]	0	-	-	-	-
Southern red-backed vole (WA)[2]	-	-	-	--	--
Western red-backed vole (OR)[2]	-	-	-	--	--
Creeping vole[1]	0, +	+	+	++	++
Amphibians					
Northwestern salamander	0	-	-	--	--
Rough-skinned newt	0	-	-	--	--
Ensatina	0	0, -	0, -	-	-
Tailed frog (WA)	-	--	--	---	---

[1] Generalist species or species associated with early-successional stages of forest development
[2] Species associated with closed-canopy forests
[3] Arboreal or semi-arboreal species

TABLE 2. Within-block pre-treatment rank abundance of 17 songbird species with >30 detections/block/year in the DEMO experimental green-tree retention study in Oregon and Washington during 1995 and 1996. Abundance is inversely correlated with rank (i.e., 1 indicates highest abundance).

		Oregon Blocks				Washington Blocks			
Species	Common Name	Watson Falls[1]	Little River	Layng Creek	Dog Prairie[2]	Butte	Little White Salmon	Paradise Hills	Capitol Forest
Dendroica occidentalis/D. townsendi	Hermit/Townsend's warbler[3]	1	1	2	1	1	1	1	7
Regulus satrapa	Golden-crowned kinglet[3]	4	2	7	2	2	3	2	5
Troglodytes troglodytes	Winter wren[3]	is[4]	5	1	is	4	5	5	1
Sitta canadensis	Red-breasted nuthatch[3]	2	3	5	5	8	2	3	10
Junco hyemalis	Dark-eyed junco[3]	5	6	is	4	3	4	6	13
Certhia americana	Brown creeper[3]	6	4	4	3	5	6	4	6
Empidonax difficilis	Pacific-slope flycatcher[3]	is	9	8	is	7	12	12	2
Parus rufescens	Chestnut-backed chickadee[3]	7	7	3	is	6	8	7	4
Wilsonia pusilla	Wilson's warbler	is	is	9	nd[5]	nd	11	is	3
Catharus guttatas	Hermit thrush[3]	8	8	is	is	9	7	8	is
Empidonax hammondii	Hammond's flycatcher[3]	3	10	6	is	is	is	is	is
Oporornis tolmiei	MacGillivray's warbler[3]	9	is	10	nd	is	is	nd	is
Perisoreus canadensis	Gray jay	is	is	is	is	10	9	10	11
Ixoreus naevius	Varied thrush[3]	is	is	is	nd	is	is	9	9
Carduelis pinus	Pine siskin	is	is	is	is	11	10	11	is
Catharus ustulata	Swainson's thrush[3]	is	is	is	is	nd	is	is	8
Dendroica nigrescens	Black-throated gray warbler	nd	is	is	nd	nd	is	nd	12
Mean annual total detections		1768	1742	1550	1353	1335	1830	1641	1882

[1] 1994 and 1995 data
[2] 1996 data only
[3] Species additionally sampled with spot mapping
[4] is = insufficient sample size (i.e., < 30 detections per block)
[5] nd = not detected

show treatment effects for at least the four species found in significant numbers in all blocks.

Hermit/Townsend's warblers, golden-crowned kinglets, red-breasted nuthatches, and brown creepers were fairly abundant on all blocks in both states (Table 2). As expected, species that occupy large territories (e.g., grouse, woodpeckers, and corvids) generally were detected in small numbers and are not included in the list. Of the 15 species in Washington blocks, four were either not detected or detected only in small numbers on some blocks. This was true for seven species in Oregon.

Some elevational trends in species abundance also were evident. For example, winter wrens (*Troglodytes troglodytes*), Wilson's warblers (*Wilsonia pusilla*), and Pacific-slope flycatchers (*Empidonax difficilis*) generally were most abundant in low-elevation blocks (Capitol Forest, Layng Creek). Resulting regional and elevational differences in bird species composition and abundance between blocks in Oregon and Washington will make future analysis over the total array of treatments potentially difficult for some species.

Arboreal and Terrestrial Small Mammals

Review

The small mammal community of the Pacific Northwest is one of the richest in North America (Harris 1984, Raphael 1990). Several species, such as the Trowbridge's shrew (*Sorex trowbridgii*), shrew-mole (*Neurotrichus gibbsii*), forest deer mouse (*Peromyscus keeni*), western red-backed vole (*Clethrionomys californicus*), and red tree vole (*Phenacomys longicaudus*), occur only in western British Columbia, Washington, Oregon, or northern California (Hagmeier and Stults 1964, Simpson 1964). These species are well adapted to older forests (Harris 1984, Aubry et al. 1991) and typically occur in greatest abundance in naturally regenerated mature forests (Carey and Johnson 1995).

Arboreal and terrestrial small mammals play important ecological roles in forest ecosystems. They form key links in many food webs as consumers and prey, and are important dispersers of plant propagules (Harris 1984). For example, northern flying squirrels, red tree voles, and woodrats (*Neotoma* spp.) are primary prey for the northern spotted owl and other forest owls (Forsman et al. 1984). Some arboreal and terrestrial rodents consume the sporocarps of ectomycorrhizal fungi and disperse fungal spores and nitrogen-fixing bacteria (Fogel and Trappe 1978, Li et al. 1986) and thus represent an important link in the nutrient cycling and productivity of forests.

Arboreal and semi-arboreal species in the study areas are consistently found in closed-canopy forest that has developed beyond the stem-exclusion stage. This pattern is generally attributable to the greater compositional and structural diversity found in old forest age classes (Carey 1991, 1995). These species can, however, be relatively abundant in younger stands with diverse understory composition and woody debris legacies (Doyle 1990, Rosenberg and Anthony 1993, Carey 1995). However, they are heavily influenced by traditional forest management practices that remove part or all of the forest canopy (Carey 1991, 1995).

The diversity of terrestrial small mammals in the study areas precludes a simple generalization about abundance in relation to forest age and habitat features. Many investigators have studied small mammals in old-growth forests, in naturally regenerated younger stands, and in recent clearcuts (<20 yr old) (Hooven and Black 1976, Ramirez and Hornocker 1981, Martell 1983, Van Horne 1983, Raphael 1988, Morrison and Anthony 1989, Ruggiero et al. 1991, Carey 1995, Carey and Johnson 1995). Several species (red-backed voles, Trowbridge's shrew, shrew-moles) are most abundant in closed-canopy forests that have developed beyond the stem-exclusion stage, where sparse herb and shrub layers provide limited resources for these species. Several other species are habitat generalists (deer mouse [*Peromyscus maniculatus*], montane shrew [*Sorex monticolus*]), or are most abundant in dense, ground-level vegetation characteristic of early-successional communities and streamside areas (creeping vole [*Microtus oregoni*], Pacific jumping mouse [*Zapus trinotatus*]). Clearcut logging produces unfavorable habitat for closed-canopy species until canopy closure. Long-term adverse impacts on persistence (over several rotations) may occur if harvest techniques eliminate inputs of coarse woody debris and other resources. Conversely, high-intensity disturbances will lead to an increase of early-successional small mammal species. Generalist species also may increase in abundance with disturbance as a direct effect of habitat changes

and indirectly if the disturbance adversely affects competitors.

Although the general changes in the composition of small mammal communities can be predicted following clearcutting, (Hooven and Black 1976, Morrison and Anthony 1989) responses to less intensive harvest are not clear. Recent studies have examined small mammal response to green-tree retention harvests (Waters and Zabel 1995, Chambers 1996, Von Treba et al. 1998), but these studies were not designed to provide broad inference for Pacific Northwest species. In particular, little information is available to compare effects of dispersed vs. aggregated retention, or to predict patterns of response across a gradient of increasing disturbance intensity. Similarly, the ability of retention patches to serve as refugia for closed-canopy species is unknown.

Hypotheses

Hypothesis 1—*Abundance of arboreal rodents will decline with decreasing levels of retention of green trees, although aggregation of retention will reduce this effect (Table 1).* Decreasing retention will result in marked reduction in arboreal canopy habitat and den snags in treatment units with <40% retention (Halpern et al. 1999). Old decayed snags, which are most valuable for denning sites, will be lost in treated areas, and creation of replacement snags from sound trees will have little benefit in the short-term. Similar declining trends in the number of vegetation layers and the cover of the dominant understory shrubs (e.g., *Acer circinatum*, *Berberis nervosa*, *Gaultheria shallon* and *Vaccinium* spp.)—especially ericaceous shrubs—will contribute to the hypothesized response (Carey 1995).

Northern flying squirrels likely will show greater responses to treatments than chipmunks (*Tamias* spp.), which are semi-arboreal (Carey 1991). However, aggregation of retained trees in undisturbed refugia likely will ameliorate these effects to some extent. Declining abundances of arboreal rodents also will be associated with declines in the diversity and abundance of ectomycorrhizal fungi as a consequence of canopy removal (Cazares et al. 1999). Northern flying squirrels, which are obligate fungivores, are expected to experience greater treatment effects than chipmunks, which have more diverse diets.

Hypothesis 2—*Terrestrial small mammals associated with closed canopy (post stem-exclusion) forests will decline with increasing levels of disturbance (Table 1); treatment-level abundances will not differ between dispersed and aggregated harvests of the same intensity.* We expect clumped populations of these species will be found in retention patches of aggregate treatment units, with few individuals occupying the harvested matrix. In dispersed retention patches, these species will be found in low abundance throughout the unit.

Hypothesis 3—*Small mammal species associated with early-successional habitats and habitat generalists will increase or have no change in abundance with disturbance intensity.* The relative abundance of these species will increase with the proportion of basal area removed. Patterns of dispersion for these species will be the inverse of the patterns hypothesized for closed-canopy species.

Methods

Methods for live-trapping arboreal rodents were modified from Carey et al. (1991a). Tomahawk 201[1] traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin) were used to sample an 8 x 8 or 7 x 9 sampling grid within each treatment unit. Sampling occurred in the fall to estimate reproductive status, relative abundances, and consumption of hypogeous fungi by flying squirrels and chipmunks. Captures were reported as individuals captured per 100 trap nights, adjusted by 0.5 trap nights for sprung traps; however, mark-recapture population estimates will be made if further analysis shows that capture data can meet the proper assumptions.

Sampling for 2 wk on all units during 1994 and 1995 indicated that flying squirrel abundances were too low (averaging 0-1 squirrel per grid) in three of eight blocks for future analysis of treatment effects, and that an additional 2 wk of sampling resulted in about 25% more captures of individual squirrels. As a result, we discontinued sampling arboreal rodents in the four blocks with low to marginal abundance, but doubled the sampling period to 4 wk at the remaining four blocks. Power analysis showed that doubling the trapping sessions to 4 wk on four blocks would result in power $\geq$0.90 for detecting a 50% reduction in abundance.

To estimate the species and quantities of fungi consumed, fecal pellets were collected from flying squirrels, chipmunks, and red-backed voles on the Watson Falls block in Oregon and the Butte block in Washington. Frequency of occurrence and relative abundance of fungal spores in feces will be compared to the concurrent frequency and abundance of fungi sampled as part of the DEMO mycological studies (Cazares et al. 1999).

Pitfall traps were used to sample terrestrial small mammals at each point in the grid. Only pitfall traps were used because they sample those species whose habitat associations are least understood, i.e., the insectivores. Most other small mammal species, although less efficiently captured by pitfall traps, are generally caught in sufficient numbers for statistical analyses (Aubry et al. 1991); power analysis of preliminary pitfall captures for deer mice (*Peromyscus* spp.) showed power to be ≥0.99 for detecting 50% reductions in abundance. Power to estimate effects on Trowbridge's shrew and vagrant shrew (*Sorex vagrans*), which were more abundant than deer mice, is expected to be similar.

Pitfall traps were operated as removal traps to provide data comparable to previous studies in unmanaged forests (Ruggiero et al. 1991) and to ongoing studies in managed forests in the Pacific Northwest (K. B. Aubry, pers. comm.). Traps were partially filled with water as recommended by the American Society of Mammalogists (1987), opened for 28 days in each treatment unit, and checked once a week between September and November. Numbers caught were reported as an uncorrected catch per unit effort index (captures/100 trap nights).

Summary of Pre-treatment Results

Ten rodent species were captured using arboreal rodent trapping methods during 1995-96 (Table 3). Chipmunks were the most frequently captured group. Townsend's chipmunk (*Tamias townsendii*) was abundant on all Washington blocks and on the Layng Creek block in Oregon. The Siskiyou chipmunk (*T. siskiyou*) was the most abundant species on the Watson Falls block in Oregon. Altogether, 568 northern flying squirrels were captured. Small numbers of bushy-tailed woodrats (*Neotoma cinerea*) were captured on several blocks. Douglas' squirrels (*Tamiasciurus douglasii*) were captured infrequently on all blocks, but this species is probably underrepresented in the data due to trap avoidance (Carey et al. 1991a).

Captures of terrestrial small mammals were similar in Oregon and Washington, with shrews (*Sorex* spp.), deer mice (*Peromyscus* spp.), and

TABLE 3. Within-block pre-treatment rank abundance of rodent species captured in Tomahawk live traps in the DEMO experimental green-tree retention study in Oregon and Washington during 1995 and 1996. Capture ranks (1 = highest abundance) were determined from the total number of individuals captured for each species within a block.

		Oregon Blocks		Washington Blocks	
Species	Common Name	Watson Falls	Layng Creek	Butte	Capitol Forest
Tamias townsendii	Townsend's chipmunk[1]	na[2]	1	1	1
Tamias siskiyou	Siskiyou chipmunk[1]	1	na	na	na
Glaucomys sabrinus	Northern flying squirrel	2	2	2	2
Tamiasciurus douglasii	Douglas' squirrel	3	3	5	3
Spermophilus lateralis	Golden-mantled ground squirrel	4	--[3]	na	na
Spermophilus beecheyi	California ground squirrel	5	--	--	--
Neotoma cinerea	Bushy-tailed woodrat	6	4	3	--
Spermophilus saturatus	Cascade golden-mantled ground squirrel	na	na	4	--
Tamias amoenus	Yellow-pine chipmunk	--	--	6	--
Sciurus carolinensis	Eastern gray squirrel	--	--	--	4
Mean annual total individuals		251	286	321	153

[1] Distributions of Townsend's and Siskiyou chipmunks in Oregon according to Verts and Carraway (1998).

[2] na = species' range outside of sample blocks

[3] -- = not captured

red-backed voles (*Clethrionomys* spp.) comprising approximately 80% of the capture totals (Table 4). Rank order of mammalian captures was fairly consistent among blocks, although the southern red-backed vole in Washington had high abundance in dense-canopy, high-elevation blocks (Paradise Hills and Butte) and intermediate abundance in open-canopy (Little White Salmon) or low-elevation (Capitol Forest) blocks.

Given the pre-treatment capture totals it appears that we will have sufficient samples of Townsend's chipmunk, Siskiyou chipmunk, and the northern flying squirrel to test for treatment effects (Table 3). For the terrestrial small mammals we should have sufficient samples for Trowbridge's shrew, vagrant shrew, fog shrew (*Sorex sonomae*, after Carraway 1990), montane shrew, southern red-backed vole, western red-backed vole, deer mouse, and forest deer mouse (Table 4). Three other species (shrew-mole, creeping vole, Pacific jumping mouse) may be included in the statistical analysis depending upon their post-treatment responses.

Bats

Review

There is growing concern for the future of microchiropteran bats in intensively managed forest landscapes throughout the world (e.g., Lunney et al. 1985, Thomas 1988, Limpens and Kapteyn 1991, Thomas and West 1991). Two issues are of special importance: (1) reduction or loss of suitable day-roost sites in young forests and (2) changes in foraging ecology through alterations in the composition and abundance of prey and in the configuration of foraging space. Most work to date has addressed the first of these two issues.

The relationships of forest-dwelling bat species to forest structures and ultimately the silvicultural systems that produce them may be the least known for all vertebrate groups in the Pacific Northwest. Radiotelemetry indicates that bats use structures associated with old forests by roosting within the fissures and under the flakes of bark on large living trees and within the cracks and openings of large snags (Barclay et al. 1988,

TABLE 4. Within-block pre-treatment rank abundance of terrestrial small mammal species captured in pitfall traps for the DEMO experimental green-tree retention study in Oregon and Washington during 1995 and 1996. Abundance is inversely correlated with rank (i.e., 1 indicates highest abundance).

		Oregon Blocks				Washington Blocks			
Species	Common Name	Watson Falls	Little River	Layng Creek	Dog Prairie	Butte	Little White Salmon	Paradise Hills	Capitol Forest
Sorex trowbridgii	Trowbridge's shrew	1	1	1	1	1	1	3	1
Clethrionomys gapperi	Southern red-backed vole	na[1]	na	na	na	2	5	1	4
Clethrionomys californicus	Western red-backed vole	2	2	2	2	na	na	na	na
Sorex vagrans	Vagrant shrew	3	5	7	4	12	7	11	10
Peromyscus maniculatus	Deer mouse	4	3	4	3	5	4	6	6
Sorex sonomae	Fog shrew	5	4	3	5	na	na	na	na
Neurotrichus gibbsii	Shrew-mole	6	7	5	7	8	10	11	8
Microtus oregoni	Creeping vole	7	6	8	6	7	9	9	7
Mustela erminea	Ermine	8	10	10	10	9	11	10	11
Zapus trinotatus	Pacific jumping mouse	9	8	6	9	--[3]	--	--	--
Scapanus orarius	Coast mole	9	9	9	8	--	--	--	--
Peromyscus keeni	Forest deer mouse	na	na	na	na	3	2	2	2
Peromyscus species[2]	Juvenile deer mouse	--	--	--	--	6	3	5	3
Sorex monticolus	Montane shrew	na	na	na	na	4	6	4	5
Glaucomys sabrinus	Northern flying squirrel	--	--	--	--	10	12	8	9
Tamias townsendii	Townsend's chipmunk	--	--	--	--	11	8	7	12
Mean annual total individuals		633	1144	687	744	662	581	374	1038

[1] na = species' range outside of sample blocks

[2] Taxon not identified to species level

[3] -- = not captured in all blocks within a state

Christy 1993, Frazier 1997). When studied in forests with continuous canopy ranging from 55 to 700 yr-of-age, echolocation calls were 2.7 to 5.7 times more frequent in older (>210 yr) than in younger forest (Thomas and West 1991). When studied over the much smaller range of stand ages found on private, intensively managed forest lands (from clearcut areas to about 65 yr-of-age), echolocation calls were about two times more frequent over clearcut areas than in young forest (Erickson and West 1996).

Concomitant with greater echolocation call frequency over clearcut areas is a shift in composition of calls to a higher proportion of larger bodied, non-*Myotis* species, a pattern also found by Hayes and Adam (1996). While there is little doubt that intensive forest management can lead to loss of forest structures that are important to bats and could result in bat population decline, the effects of partial harvests and green-tree retention on bat use of forested areas are not clear (Fenton et al. 1998). Given the provision of suitable day roosts, bat populations may do quite well. Critical work on the characteristics of roosts is very recent for this region (Campbell 1993, Erickson 1993, Ormsbee 1996, Frazier 1997). No studies have addressed bat habitat use on a large-scale experimental basis.

Hypotheses

Hypothesis 1—*Use of green-tree retention units will increase with harvest intensity for non-Myotis species.* As flight space for larger-bodied and faster flying bats is created, echolocation calls of silver-haired (*Lasionycteris noctivagans*), hoary (*Lasiurus cinereus*), and Townsend's big-eared bats (*Corynorhinus townsendii*) will be detected at higher numbers. The number of echolocation calls from *Myotis* species will not change. Thus, the number of echolocation calls summed across bat species will increase with harvest intensity.

Hypothesis 2—*Feeding rates will increase with harvest intensity.* Clearcut areas function as commuting space and as marginal areas for feeding. Closed-canopy stands function primarily for roosting. As harvest intensity increases, the frequency of "feeding buzzes" (a characteristic call indicating prey capture) should increase.

Methods

Indices of bat activity were estimated with automated divide-by-N detectors (Anabat II detectors and delay switches, Titley Electronics, Ballina, N.S.W., Australia). The systems were set to record at dusk and shut down 8-9 hr later. Several detectors were operated simultaneously at blocks within each state. Each block was surveyed for a 2-day period each month. Sampling for echolocation calls began in late June or early July depending upon the timing of warm weather. We found that a minimum of 6 nights of sampling per site (excluding windy or rainy nights) was necessary to account for the high variation in recorded calls among nights. Although it is generally not possible to distinguish repeated calls made by an individual bat from individual calls of many bats, the technique offers a very good method for determining presence, relative use, and behavior (feeding vs. passover) of bats in an area.

To provide information on age, sex ratios, reproductive condition, and species identification of *Myotis* species, we captured bats near habitual flyways, streams, and ponds with mist nets and collapsible harp traps (Kunz and Kurta 1988). Upon release, echolocation calls of captured bats were recorded to augment our library of reference calls.

Summary of Pre-treatment Results

At present we can identify the following five species or species groups (Erickson and West 1996): (1) big brown bat, (2) hoary bat, (3) silver-haired bat, (4) Townsend's big-eared bat, and (5) *Myotis* species (*M. evotis, M. volans, M. keenii, M. ciliolabrum, M. californicus, and M. lucifugus*).

A total of 3,924 calls were detected during the pre-treatment sampling. In Washington, the *Myotis* group accounted for 98% of the 2,102 recorded detections (Table 5). Other species were rarely detected. Detections at the Little White Salmon block accounted for over half (62%) of all detections in Washington and 33% of calls for both states. In Oregon, the *Myotis* species group accounted for 97% of the 1,822 recorded calls.

Nightly activity was highest on the Little White Salmon block, which has relatively open-canopy stands, with an average of ≥17 calls per night. This range of activity is as high as that found in old-growth (Thomas and West 1991). The Little River block was the second most active site with just over eight calls per night. The least active blocks were the relatively closed-canopy Butte and Paradise Hills blocks with <3 calls per night.

TABLE 5. Pre-treatment mean detection rate (echolocation calls/night), and standard error of mean, for all bats, all *Myotis* species, and all non-*Myotis* species in DEMO experimental green-tree retention blocks in Oregon (1995 and 1996) and Washington (1995).

Block	Total $\bar{x}$ (se)	*Myotis* $\bar{x}$ (se)	Non-*Myotis* $\bar{x}$ (se)
Oregon			
Watson Falls	7.89 (11.22)	7.71 (11.20)	0.11 (0.72)
Little River	8.21 (10.39)	8.14 (10.32)	0.07 (0.30)
Layng Creek	4.92 (6.43)	4.43 (5.66)	0.45 (2.55)
Dog Prairie	4.06 (9.97)	4.06 (9.97)	0
Washington			
Butte	2.53 (11.04)	2.45 (10.98)	0.06 (0.23)
Little White Salmon	17.81 (29.58)	17.26 (29.16)	0.51 (2.99)
Paradise Hills	1.56 (2.86)	1.55 (2.96)	0.04 (0.19)
Capitol Forest	6.90 (14.87)	6.90 (14.87)	0

As expected, feeding activity was low within all blocks. Of the 3,924 detections, only 35 were identified as feeding activity. Little White Salmon had the highest number of feeding buzzes, accounting for 66% of the feeding activity.

Amphibians

Review

In regions west of the Cascade crest, amphibians dominate the Pacific Northwest herpetofauna. Not only are there more species of amphibians than reptiles, but they are more distinctive in their endemism (Nussbaum et al. 1983). In headwater streams and riparian areas of the Pacific Northwest, amphibian adults and larvae are the top predators, easily exceeding the numbers and biomass of other forms (Bury 1988). Densities of amphibians can be very high, up to 12 per m^2 in moist areas (Leonard et al. 1993).

Several amphibian taxa are being revised and a number of cryptic species have been described (Good 1989, Good and Wake 1992, Green et al. 1997). Recent identification of new species underscores the disjunct nature of amphibian distributions and the potential for extinction. Although there have been studies of habitat relationships in unmanaged forests for the systematically stable species of the region (Raphael 1988, Aubry and Hall 1991, Corn and Bury 1991, Gilbert and Allwine 1991b), we know little about habitat associations for many of the newly identified species in unmanaged forests. Information in managed forests is particularly sparse for most species. Well-replicated studies of amphibian occurrence in managed forest are needed to investigate the effects of several commonly employed silvicultural practices, including short-rotation harvest, thinning, and green-tree retention. Several species have special status in Oregon and Washington: Cascade frog (*Rana cascadae*), tailed frog (*Ascaphus truei*), spotted frog (*Rana pretiosa*), clouded salamander (*Aneides ferreus*), Oregon slender salamander (*Batrachoseps wrighti*), torrent salamanders (*Rhyacotriton cascadae* and *R. variegatus*), Larch Mountain salamander (*Plethodon larselli*), Dunn's salamander (*P. dunni*), and Van Dyke's salamander (*P. vandykei*). Information from our studies will be important for conservation of these sensitive species.

Hypotheses

Hypothesis 1—*Abundance of amphibians will decline with harvest intensity.* We expect a general decline for all species with increasing harvest intensity, with the exception of the western red-backed salamander (*Plethodon vehiculum*) in Washington where the species has shown an ability to persist in clearcut areas. We expect a sharp decline in species richness, but this may occur over a longer time frame than the initial 2-yr post-harvest sampling period. Several amphibian species are long lived and are capable of withstanding adverse conditions for prolonged periods. Thus, we may see a lag response for this pattern, underscoring the need to resample these sites in the future (perhaps at 5 and 10 yr after the initial post-harvest sampling).

Hypothesis 2—*Amphibians will persist in forest patches in aggregated retention units, but most species will decline in harvested areas within aggregated retention units and in dispersed retention units.* We expect that the retained forest patches may be sufficient to permit survival of a portion of the original amphibian community, perhaps until the forest canopy closes again. We expect the numbers of amphibians persisting in the forest patches to be positively correlated with the total area remaining in patches.

Hypothesis 3—*Individuals captured in the harvested portions of the aggregated retention units and in the 15% dispersed retention units will show poorer body condition compared to individuals found within the forest patches or in the 40% dispersed retention units.* Adverse conditions in harvest areas should lead to poor body condition for individuals residing there. We would expect reduced reproduction and lower than expected values for body-condition indices (such as a regression of weight vs. snout-vent length).

Methods

Amphibians were sampled concurrently with terrestrial small mammals during fall using pitfall traps. Traps were opened after the onset of fall rains when amphibian surface activity increases from the relative inactivity of summer. After identifying species and recording information on body dimensions, mass, sex and reproductive condition, amphibians were toe-clipped and released or held under cool, moist conditions for the remainder of the sampling periods then returned to their point of capture. As with small mammals, numbers caught were expressed as an uncorrected catch of individuals per unit effort index (captures/100 trap nights).

Pitfall trapping is a good technique for capturing surface-active amphibians, but is not very effective at sampling species that limit their movements to surface cover or the interior of large woody debris. Fortunately, only two species limit their surface activity, the clouded salamander and the Oregon slender salamander, both of which occur only in Oregon. Time-constrained searches and cover-board sampling techniques to target these species initially were planned, but were not conducted because of budget constraints and the localized distributions of the species.

Summary of Pre-treatment Results

The rank ordering of amphibian captures showed considerable variation among blocks and between states (Table 6). Amphibian abundance and diversity were about two times higher in Washington than in Oregon. Five species were common to all blocks in Washington, but only two species were present on all blocks in Oregon. In Washington, species composition varied considerably among blocks (Table 6). This high variability will make statistical detection of post-treatment effects difficult. However, the ensatina (*Ensatina eschscholtzii*), which comprised 54% of all amphibian captures across the eight blocks should be a suitable species for detecting treatment effects across both states. In Washington, the northwestern salamander (*Ambystoma gracile*) and the tailed frog were also common enough to suggest that treatment effects will be detectable.

Limitations and Challenges

In an undertaking of this kind and magnitude one expects challenges. We have experienced several difficulties thus far; many were expected and others were not. For example, we anticipated that the patchiness of species' distributions would make uniform replicates impossible. There are species in each vertebrate group that are found only in subsets of the study blocks. This will result in lower power for treatment comparisons. In addition, the scale of silvicultural operations does not always mesh well with the scales of species' biology. Given the small size of harvest units relative to the home ranges of larger-bodied species, some species will not respond exclusively to the effects of the experimental treatments. They may show partial responses to the treatments, but may be influenced by conditions adjacent to the treatment areas. Our choices of species for the study were made partly with this in mind. We chose those species for which we had the best chance of measuring a response attributable to the treatments, i.e., those species with limited movement or those tied to small areas by seasonal territoriality. This approach cannot be entirely successful, and while the scaling will be acceptable for small mammals, amphibians, and several avian species, it may be unsatisfactory for others such as the larger cavity-nesting birds.

TABLE 6. Within-block pre-treatment rank abundance of amphibian species captured in pitfall traps for the DEMO experimental green-tree retention study in Oregon and Washington during 1995 and 1996. Abundance is inversely correlated with rank (i.e., 1 indicates highest abundance).

		Oregon Blocks				Washington Blocks			
Species	Common Name	Watson Falls	Little River	Layng Creek	Dog Prairie	Butte	Little White Salmon	Paradise Hills	Capitol Forest
Ensatina eschscholtzii	Ensatina	1	3	1	1	2	1	5	1
Plethodon vehiculum	Western red-backed salamander	--[1]	--	2	3	--	10	--	2
Ascaphus truei	Tailed frog	--	--	--	--	1	3	1	6
Ambystoma gracile	Northwestern salamander	2	1	5	2	3	2	2	3
Taricha granulosa	Rough-skinned newt	3	2	3	--	6	5	4	4
Ambystoma macrodactylum	Long-toed salamander	--	--	--	--	--	4	7	--
Rhyacotriton cascadae	Cascade torrent salamander	--	--	--	--	--	8	3	--
Rana aurora	Red-legged frog	nd[2]	nd	nd	nd	5	10	11	5
Rana cascadae	Cascades frog	nd	nd	nd	nd	--	6	6	--
Hyla regilla	Pacific tree frog	4	--	--	3	4	10	9	--
Rana spp.	Unidentified frog	5	6	--	3	nd	nd	nd	nd
Dicamptodon tenebrosus	Pacific giant salamander	--	5	6	--	--	8	8	--
Bufo boreas	Western toad	--	--	--	--	7	6	9	--
Aneides ferreus	Clouded salamander	--	4	4	3	na[3]	na	na	na
Plethodon dunni	Dunn's salamander	--	--	6	--	na	na	na	na
Mean annual total individuals		55	114	90	140	56	204	132	467

[1] -- = not captured

[2] nd = *Rana* species not differentiated in Oregon blocks

[3] na = species' range outside of sample blocks

We primarily will use indices of abundance as treatment response variables rather than indicators of realized fitness (e.g., juvenile survival). However, because density or abundance estimates can be misleading indicators of habitat quality (Van Horne 1983), we will attempt to estimate indices of fitness for vertebrates when feasible. Nest searches and territory mapping in conjunction with counts will help to determine treatment effects on the number of breeding bird territories. Determination of the age class and reproductive condition of small mammals and amphibians captured in pitfall traps will provide estimates of age-class distributions and reproductive condition in treatment units. Age-class distributions and estimates of reproductive condition in live-caught rodents (chipmunks, flying squirrels) will help to indicate realized fitness relative to treatments. The presence or absence of bat roosts will indicate sensitivity of bats to treatments.

The costs associated with these studies are very high. It has been necessary to rework the sampling design in response to budgetary shortfalls. These considerations have led to reduced sampling efforts for arboreal rodents (reductions in trapping intensity per period and loss of seasonal sampling), small mammals (elimination of simultaneous live trapping), and amphibians (elimination of time-constrained searches).

Our final concern recognizes that not all responses to treatments will occur within the initial 2-yr post-harvest sampling period. We expect lag responses for several species groups within the amphibians, arboreal rodents, and birds. We expect species packing in the aggregated retention patches for species in all of these groups, a phenomenon that may not begin to dissipate until the second or even third post-harvest year. These concerns point to the need for intensive, long-term sampling to understand how key forest species or species groups will respond to stand-level manipulations, the effects of which may be manifested over decades. Funding agencies must likewise be willing to provide continuing support if they wish to successfully manage for species whose responses to harvest activities may be dynamic over long periods of time.

Acknowledgements

We thank the vital and tireless work of personnel on the Umpqua and Gifford Pinchot National Forests and the Capitol State Forest: Brenda Woodard, Rick Abbott, Cindy Lagoudakis, Barbara Fontaine, and Wayne Kleckner (Umpqua National Forest); Jim White, Debbie Couche, Sue MacMeeken, Jon Nakae, and Ed Tompkins (Gifford Pinchot National Forest); and Richard Bigley (Capitol State Forest). We could not have accomplished the collection and analysis of data without the assistance of Chris Maguire, Tom Manning, Jeff Feen, Rebecca Thompson, and Tiffany Church. Larry Bednar did the power analyses. Jim White and three anonymous referees provided critical reviews of this paper. We benefited greatly from the insightful editorial comments of Martin Raphael and Charles Halpern. This is a product of the Demonstration of Ecosystem Management Options (DEMO) study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources.

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Endnote

[1] The use of trade or firm names is for reader information only and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

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Interaction of Fungal Sporocarp Production with Small Mammal Abundance and Diet in Douglas-fir Stands of the Southern Cascade Range

Abstract

Small mammal population densities are highly variable across forest stands and landscapes. The species composition and abundance of ectomycorrhizal fungi (EMF) may influence the ability of forests to provide suitable habitat for small mammals. Identification and interpretation of changes in the abundance of these organisms, or in their inter-relationships due to experimental harvest, require that we first identify the patterns and potential causes of natural variability in the pre-harvest communities. Pre-treatment data were gathered from the Watson Falls block of a green-tree retention experiment to establish baseline conditions. The six experimental treatments that comprise this block lie in two spatially distinct areas that differ in environment and forest composition. The initial variability in EMF, small mammals, and their relationships was documented. Three primary questions are addressed in this paper: (1) Are the abundance and species composition of EMF sporocarps similar between the two areas of the Watson Falls block? (2) How does sporocarp consumption vary among small mammal species and by area? (3) For common truffle genera, is sporocarp biomass correlated with the spore frequency of those genera in small mammal diets? The Watson Falls block was found to have spatial and temporal variation in EMF production, small mammal mycophagy, and small mammal abundance. However, truffles were consistently the primary food item in the diet of all three small mammal species in this study. Small mammals are potentially important agents of truffle dispersal into disturbed areas where EMF are locally extirpated. This study furthers knowledge of the role of small mammal mycophagy in the functioning of forest ecosystems.

Introduction

Ectomycorrhizal fungi (EMF) form symbiotic relationships with the roots of trees and other vegetation. Trees supply carbon from photosynthesis to the fungi, in turn, EMF absorb minerals and nutrients from the soil and transfer them to tree roots (Smith and Read 1997). Mycorrhizae are essential for survival and growth of most coniferous forest trees and other shrubs and herbaceous vegetation (Fogel and Trappe 1978).

Ectomycorrhizal fungal species vary in their abundance and phenology of fruiting (Fogel 1981; Hunt and Trappe 1987; Luoma 1988, 1991; Luoma et al. 1991, 1997; Amaranthus et al. 1994; North et al. 1997; States and Gaud 1997) and in the nutritional value of their fruit bodies (Fogel and Trappe 1978). Various abiotic and biotic factors influence the fruiting of EMF (Villeneuve et al. 1991). Sporocarps are non-uniform in distribution, varying from a few, scattered fruitbodies to concentrated clusters of numerous fruitbodies (North et al. 1997, States and Gaud 1997, Waters et al. 1997). In planned experiments, documentation of existing fruiting patterns is critical to the interpretation of changes that may result from manipulation of treatment units.

Small mammals are integral components of many forest ecosystems including the Douglas-fir (*Pseudotsuga menziesii*) forests that dominate much of the western Cascade landscape. Numerous species of forest-dwelling, small mammals rely on the fruiting bodies of EMF as a primary source of food (Fogel and Trappe 1978, Maser et al. 1986, Maser and Maser 1988, Hall 1991, Waters and Zabel 1995). A food-web linkage of particular interest is between the endangered northern spotted owl (*Strix occidentalis caurina*) and the northern flying squirrel (*Glaucomys sabrinus*). The northern spotted owl feeds primarily on flying squirrels over most of their range (Forsman et al. 1984, Thomas et al. 1990, Carey 1991). Northern flying

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squirrels, in turn, require truffles, below-ground fruiting bodies of EMF, as their primary food source (Maser et al. 1985, Carey 1995). Other mycophagous (fungus eating) small mammals, such as chipmunks (*Tamias* spp.) are prey for raptors (e.g., goshawks) and mammalian carnivores (e.g., marten and fisher) (Fogel and Trappe 1978, McIntire 1984, Hayes et al. 1986, Carey 1991).

The presence and abundance of EMF species may change during forest development (Trappe 1977, Mehus 1986, Termorshuizen 1991). Truffle fungi are primarily dispersed by small mammals that eat the sporocarps and subsequently disperse spore-packed fecal pellets (Fogel and Trappe 1978, Maser and Maser 1988). The level and pattern of structural retention in harvest units may influence small mammal species directly, thereby indirectly influencing spore dispersal of EMF. Green-tree retention may also influence the composition, abundance, and fruiting of EMF and thus indirectly influence the abundance of small mammals *via* effects on their food sources.

Studies of animal mycophagy are mainly based on stomach content or fecal pellet analysis (Fogel and Trappe 1978, Maser et al. 1978, Maser and Maser 1988, Carey 1995, Waters and Zabel 1995). These analyses can provide an accurate record of an animal's previous meal. Fecal sample analysis provides a non-lethal method for long-term and integrated studies of diet habits. Forest-dwelling small mammal species that depend upon fruiting bodies of EMF contain a diverse array of truffle genera in their fecal material (Maser et al. 1978). Small mammal population densities are highly variable across stands and landscapes (Carey et al. 1992, Rosenberg and Anthony 1992, Witt 1992) and the species composition and abundance of EMF fruiting bodies may influence the ability of forests to provide suitable habitat for small mammals. Identification and interpretation of changes in the abundance of these organisms, or of their inter-relationships due to forest harvest, require that we first identify the patterns and potential causes of natural variability in the pre-harvest communities.

The high diversity of EMF in forests of the Pacific Northwest suggests that habitats and environmental conditions are also diverse. While some EMF may thrive in intensively managed forests, most are likely adversely affected by such management (Amaranthus and Luoma 1997). A diverse mosaic of host species, habitats, and structures promote EMF diversity at the scale of landscapes. Variation in communities of EMF will reflect variation in forest type, successional stage, and the distinctive assemblages of plants and microhabitats within each of these. Silvicultural practices can be used to create habitat conditions that maintain or increase EMF diversity. For example, leaving large trees following regeneration harvests ("green-tree" retention) maintains an energy source for certain EMF species and provides for future recruitment of coarse woody debris, an important habitat component for some EMF (Amaranthus et al. 1994).

Until recently, limited consideration has been given to the conservation of EMF, despite their known ecological importance. The Northwest Forest Plan (USDA and USDI 1994a) now directs forest managers to incorporate rare species, including fungi, into future forest management activities. The standards and guidelines of the Plan require that federal ecologists and botanists create and maintain databases of know sites of rare fungi, and that they develop species or area management plans for these taxa (USDA and USDI 1994b). The report lists 527 species of fungi that are thought to be closely associated with late successional forests; approximately 80% of these are thought to be EMF. Studies of the spatial and temporal distributions of EMF and of their consumption by small mammals in unmanaged forests are a necessary first step if we are to understand the consequence of future management practices for these critical elements of forest ecosystems.

In this paper we describe some of these relationships in forests that will be harvested as part of the Demonstration of Ecosystem Management Options (DEMO) study (Aubry et al. 1999). The strong contrasts in levels and patterns of canopy cover produced by the six retention-harvest treatments are likely to influence habitat features and environmental conditions that in turn will affect populations of EMF and small mammals. However, initial differences in the distribution and abundance of EMF and small mammals may have equally important effects on post-treatment responses.

The six experimental units that we consider in the current study (the Watson Falls block) lie in two spatially distinct areas that differ in envi-

ronment and forest composition. Thus, it is necessary to quantify the initial variability in EMF, small mammals, and their interactions to facilitate the separation of treatment-effects from any effects due to pre-harvest differences. To this end, we pose three fundamental questions about the spatial and temporal variation of EMF sporocarps and their consumption by small mammals prior to forest harvest: (1) Are the abundance and species composition of EMF sporocarps similar between the two areas of the Watson Falls block? (2) How does sporocarp consumption vary among small mammal species and by location? (3) For the common truffle genera, is sporocarp biomass correlated with the frequency of spores found in the fecal material of small mammals?

Similar studies will be conducted following harvest thus yielding information on how levels and patterns of green-tree retention alter the abundance and distribution of EMF and of the small mammals that consume these species. Both sets of studies are critical as forest managers seek to incorporate basic ecological knowledge into forest management policies and practices.

Methods

Experimental Design

The Demonstration of Ecosystem Management Options (DEMO) study consists of six green-tree retention treatments replicated at eight geographic locations (blocks) in western Oregon and Washington (Aubry et al. 1999). The treatments consist of four levels of live tree retention (15, 40, 75, and 100% of existing live-tree basal area), with two patterns of retention (aggregated and dispersed) applied to the 15 and 40% retention treatments. The aggregated pattern consists of residual trees retained in 1-ha circular patches; the dispersed pattern consists of residual trees uniformly dispersed throughout the unit (see Aubry et al. [1999] for details).

Study Area

Three treatment units were established in each of the two primary study areas that comprise the Watson Falls block of the DEMO experiment (see Figure 3 of Aubry et al. [1999]). The two areas, named for local geographic features, Toketee Airstrip and Mowich Park, lie approximately 12 km apart with an elevational difference of about 350 m (Table 1). Both areas are comprised of 110- to130-yr-old forests dominated by Douglas-fir that originated following wildfire. Other tree species vary in importance among treatment units (Table 1).

Watson Falls lies northwest of Crater Lake National Park within the zone of heavy deposition of volcanic ejecta that originated from the eruption of Mt. Mazama 7,000 yr B.P. (Baldwin 1981). Thus, soils are deep (1.0-2.4 m), well-drained, loamy sands derived from volcanic ash and pumice. Surface soils contain low levels of organic matter, clay compounds, nitrogen, calcium, and magnesium (Radtke and Edwards 1976). The terrain is flat to gently sloping. The climate is moderate, with warm dry summers and cool wet winters. Precipitation falls in equal proportions as rain and snow at the Airstrip units, but primarily as snow at the Mowich units. Annual precipitation averages ca. 1,525 mm (U.S. Weather Service records for Lemolo Lake).

TABLE 1. Ecological and physiographic characteristics of the six treatment units at Watson Falls. Data are from the Diamond Lake Ranger District, Toketee, Oregon and Halpern et al. (1999).

	Airstrip Units			Mowich Units		
Treatment Unit	2	5	6	1	3	4
Overstory species[1]	PSME, ABCO, PIPO, PIMO	PSME, ABCO, PIPO, TSHE	PSME, ABCO, PIPO, TSHE	PSME, ABCO, TSHE	PSME, ABCO, TSHE, PIMO	PSME, ABCO, TSHE, ABMAS
Basal area (m^2/ha)	36.1	51.6	45.4	43.7	47.7	60.3
Mean DBH (cm)	37.1	48.2	40.8	40.7	40.5	43.8
Age (yr)	110	130	130	110	130	110
Slope (%)	0-5	0-5	0-5	0-10	0-10	0-10
Elevation (m)	945	945	945	1311	1311	1189

[1]Major tree species in order of decreasing dominance and coded as: ABCO = *Abies concolor*, ABMAS = *Abies magnifica* var. *shastensis*, PIMO = *Pinus monticola*, PIPO = *Pinus ponderosa*, PSME = *Pseudotsuga menziesii*, TSHE = *Tsuga heterophylla.*

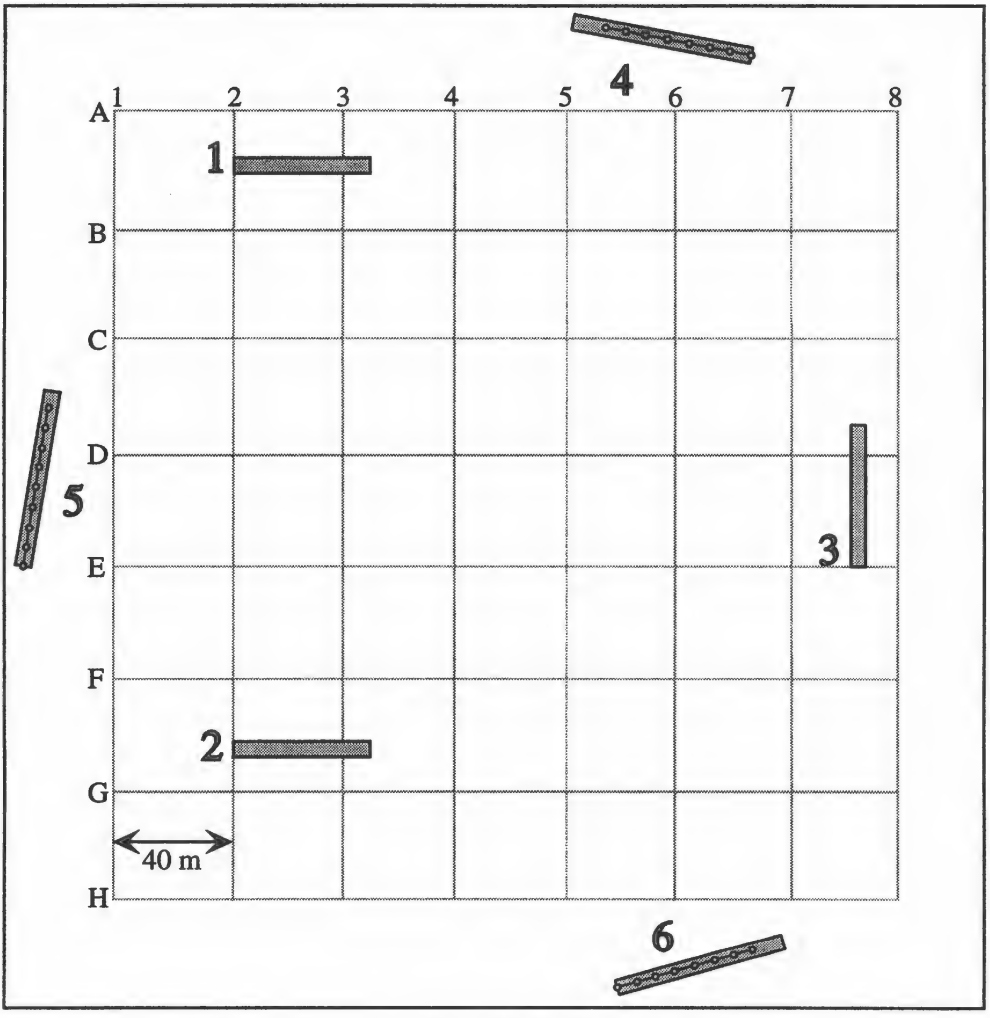

Figure 1. Schematic of sample plot layout for fungi. Plots were dispersed throughout each experimental unit. Three, permanent, 2 x 50 m mushroom sample plots (numbered 1–3) were located within the primary sampling grid (8 x 8 at 40-m spacing). Three transient, 2 x 50 m mushroom plots (numbered 4–6) were established at different locations around the grid and were replaced each sample season. Transects located down the center of the non-permanent mushroom plots contained, respectively, 8, 9, and 8, circular 4–m^2 truffle plots for a 100 m^2 total sample area. Truffle plots were placed at 6-m intervals along each transect.

Sampling of Fungal Sporocarps

Sporocarps of EMF were sampled from all treatment units during October 1993 and June 1994. These are the peak fruiting times for EMF in our region. Mushroom species were collected from 6 strip plots (2 x 50 m) per treatment unit for each seasonal sample (Figure 1). Three of the strip plots were permanently installed and were placed systematically to maintain a dispersed sample pattern. The remaining three plots were also systematically located within each unit, but were used only once during each seasonal sample; three new locations were chosen the following season. Use of the temporary strip plots increased the area and

diversity of habitat sampled. All sporocarps of EMF mushrooms were collected from the plots and distinguishing field characteristics noted. In the field facility or laboratory, sporocarps were identified to genus or species, dried, and weighed to the nearest 0.01 g to determine biomass.

Truffles were collected from 25, circular 4-m^2 plots in each treatment unit, yielding a total sample area of 100 m^2 each season. Truffle plots were placed every 6 m along a transect within the three temporary mushroom strip plots (Figure 1). In each truffle plot, the forest floor was raked to a depth of 5–10 cm, exposing sporocarps in the upper soil layers. Distinguishing field characteristics such as handling reaction and odor were noted. In the laboratory, sporocarps were identified to species, dried, and weighed to the nearest 0.01 g to determine biomass.

Sampling of Arboreal Rodents and Small Mammals

Within each of the treatment units, arboreal rodents and small mammals were sampled using an 8 x 8 or 7 x 9 trapping grid with a 40-m spacing between grid points and a buffer of at least 50 m between stand edges and the trapping grid. Animal abundance was determined from first captures only.

Arboreal Rodents

Arboreal rodents were sampled using the methodology of Carey et al. (1991). Two Tomahawk 201 live traps were placed at each grid point. One trap was placed 1.5 m above ground on a tree, and the second at the ground next to a natural drift fence (e.g., log or snag). All traps were placed within 10 m of the grid point. Traps were covered with a waxed carton to protect animals from rain. A nest box containing polyester batting and bait (a mixture of peanut butter, molasses, and oats) was placed in each trap to provide shelter, minimize hypothermia, and prevent starvation.

Arboreal rodents were trapped for two consecutive 4-day periods in September 1993 and June 1994. Total number of trap nights per treatment unit per sample season was 1024 for treatment units with an 8 x 8 grid spacing and 1008 for those with a 9 x 7 spacing.

Small Mammals

Small mammals were sampled using Sherman live traps (8 x 9 x 23 cm) and non-fatal pitfall traps (two No. 10-tin cans, stacked and joined with duct tape). Sherman traps were placed 10 m apart on a 10 x 10 grid within the larger permanent grid system for a total of 100 traps per stand. We used a subset (36) of the permanent grid points for pitfall traps. Both types of traps were placed within 3 m of each grid point along a natural drift fence. Sherman traps were covered with a waxed carton sleeve to provide insulation and shelter and polyester batting was added to minimize hypothermia. A plastic collar nested in the top of the pitfall trap prevented animals from escaping. A waxed carton containing polyester batting was placed in the bottom of each pitfall trap to provide insulation. All traps were baited with a mixture of peanut butter, molasses, and oats.

Small mammals were trapped for two consecutive 4-day periods in October 1993. The total number of trap nights per stand was 1088 (800 for Sherman traps, 288 for pitfall traps).

Diet Analyses

Fecal pellets from trapped northern flying squirrels, Siskiyou chipmunks (*Tamias siskiyou*), and western red-backed voles (*Clethrionomys californicus*) were collected from individuals that had been captured for the first time during both 4-day trapping intervals, and from all captures on the first capture day of the second week (we assumed the 3-day period between trapping sessions was adequate for bait to pass through the animal). Fecal pellets were taken directly from individual animals or, if pellets fell during handling, they were collected only from clean, dirt-free surfaces to avoid introduction of extraneous spores or plant material into the sample. One to five fecal pellets were obtained from each individual and were placed in paper envelopes labeled with collection information. Fecal pellets of Siskiyou chipmunks and western red-backed voles were not collected during the spring sample period.

In the laboratory, two samples of pooled fecal pellets were prepared for each small mammal species from each of the six treatment units (following Method 2 of Colgan et al. [1997]). Each pooled sample consisted of pellets randomly selected from three to six individuals. Pooling reduces

the time required to collect and process samples, and is efficient for examining treatment-level responses where among-individual variation is not of interest. Each pooled sample was placed in a small vial with two or three drops of 95% ethanol to dissolve lipid layers of viruses. Four to five drops of distilled water were then added to rehydrate the samples for 48 hr at room temperature. Pellets were macerated and mixed thoroughly. Three drops of the resulting suspension were placed on a microscope slide. Two drops of Melzer's reagent (iodine, potassium iodide, and chloral hydrate in aqueous solution) were added and covered with a cover slip. Three slides were prepared in this manner for each pooled fecal sample.

For each of the 3 slides, 25 randomly selected fields of view were examined at 400x magnification with a compound microscope. Fungal spores were identified to genus according to Castellano et al. (1989). It is difficult to distinguish between the closely related genera *Rhizopogon* and *Truncocolumella* solely by spore morphology; thus these taxa were grouped in subsequent analyses. In effect, this grouping affects only fall data because *Truncocolumella* does not fruit in the spring (Luoma 1988). Plant material (e.g., seed parts, pollen, and other vegetative material identified by morphology and the presence of chloroplasts) was also identified. Frequency of each item of the diet (e.g., spore type or plant material) was calculated as the percentage of occurrence of a particular food type from the 75 possible fields in each pooled fecal sample.

Statistical Analyses

Statistical comparisons of EMF sporocarp biomass, small mammal abundance, or frequency of dietary items in small mammal fecal pellets were conducted using two-way or one-way analysis of variance (ANOVA). Main effects for these ANOVAs were area, animal species, or season. Data were variously transformed to more closely meet the assumptions of normal distribution and constant variance (Sabin and Stafford 1990). Sporocarp biomass was log (*Gautieria*, *Hysterangium*, *Rhizopogon/Truncocolumella*, total truffles) or square root (Boletaceae, Cortinariaceae, total mushrooms) transformed. Sporocarp biomass variables that could not be successfully transformed to meet the assumptions of normal distribution and constant variance (as measured by skewness and kertosis) were rank transformed (Aphyllophorales, Russulaceae, other mushrooms, *Leucogaster*, other truffles). Northern flying squirrel and Siskiyou chipmunk abundance values were square-root transformed. Western red-backed vole abundance was log transformed. Dietary item variables were all rank transformed. Fisher's protected least significant difference was used as a multiple comparison procedure ($p \leq 0.1$) only when the overall ANOVA p value was ≤ 0.15. Given the numerous ANOVAs conducted, findings of statistical significance should be interpreted with caution.

Abundance of truffles may affect the amount of plant material that mycophagous animals consume. Regression analysis was used to test the relationship between truffle sporocarp biomass produced in a unit and plant material frequency recorded from fecal pellet analysis of the three small mammal species. Plant material frequency values were log transformed.

Because the assumptions of normal distribution and constant variance could not be met by transformation of truffle spore frequency values, non-parametric correlation was used to test the relationship between truffle standing-crop biomass and mean frequency of truffle spores in fecal pellets. In all analyses, *Rhizopogon* and *Truncocolumella* sporocarp biomass was combined, consistent with the procedure used in identifying spores from fecal pellets (above).

Results

Fungal Biomass

Peak seasonal truffle standing crop biomass exceeded that of ectomycorrhizal mushroom biomass in both fall 1993 and spring 1994 (Table 2). Over 85% of the total EMF sporocarp standing crop biomass was composed of truffles. *Rhizopogon/Truncocolumella* had the greatest sporocarp biomass of all groups in fall 1993 (Table 2) and *Gautieria* in spring 1994 (Table 2).

Sporocarp biomass was different ($p \leq 0.10$) for some truffle or mushroom species groups between the Airstrip and Mowich areas (Table 2). Seasonal differences for Russulaceae, *Hysterangium*, *Leucogaster*, and *Rhizopogon/Truncocolumella* did not vary between areas (Table 2).

Sporocarp biomass did show an interaction between season and location (Airstrip and Mowich) for Boletaceae, Cortinariaceae, total mushrooms, *Gautieria*, other truffles, and total truffle biomass

TABLE 2. Mean standing-crop sporocarp biomass (g/ha dry weight) (± 1 SE) and ANOVA results in two study areas at Watson Falls and for the two seasons sampled, fall 1993 and spring 1994; n = 6.

Fungal Group	Area			Season		
	Airstrip	Mowich	p[1]	Fall	Spring	p
Mushrooms						
Aphyllophorales	128 (100)	341 (147)	0.19	252 (106)	217 (157)	0.31
Boletaceae[2]	49 (28)	58 (28)	0.74	50 (28)	58 (28)	0.71
Cortinariaceae[2]	28 (6)	106 (29)	0.01	36 (13)	98 (31)	0.02
Russulaceae	56 (53)	174 (126)	0.79	229 (123)	1 (1)	0.002
Other mushrooms	46 (20)	29 (23)	0.57	18 (9)	57 (27)	0.67
Total mushrooms[2]	307 (99)	708 (148)	0.03	585 (102)	430 (187)	0.17
Truffles						
Gautieria[2]	508 (216)	2278 (1440)	0.82	77 (52)	2710 (1318)	0.002
Hysterangium	427 (197)	913 (460)	0.49	85 (55)	1255 (365)	0.007
Leucogaster	133 (76)	420 (228)	0.34	32 (32)	521 (203)	0.004
Rhizopogon/ Truncocolumella	1509 (1054)	1394 (513)	0.62	2474 (971)	428 (125)	0.03
Other truffles[2]	80 (38)	1106 (666)	0.15	68 (44)	1117 (662)	0.03
Total truffles[2]	2655 (979)	6111 (2260)	0.11	2736 (984)	6031 (2282)	0.12

[1] p values from ANOVA based on transformed data.

[2] Significant area-by-season interaction precludes simple main effects comparisons. See Table 3 for detailed interaction effects.

(Table 3). Total ectomycorrhizal mushroom biomass was significantly lower in the Airstrip area in spring 1994 (Table 3). More than 92% of the sporocarp biomass in spring 1994 was from truffles and total truffle biomass was significantly greater in the Mowich area (Table 3).

Small Mammal Diets

Spores from a total of 11 truffle genera were detected in the fecal pellets of the three small mammal species. Four genera were encountered with frequencies ≥10% (Table 4) and were considered the major food items for analytical purposes. In contrast, the frequency of mushroom spores in fecal pellets was very low; thus, mushrooms were dropped from the analyses of dietary patterns. Spores from the mushroom groups Aphyllophorales and Russulaceae were not detected in fecal pellets despite their common fruiting in all stands (Table 2).

Fall

In fall 1993, *Rhizopogon/Truncocolumella* truffles were the dominant food items in the diets of all three mammal species (Table 4) and showed no differences in occurrence among them (Table 5).

TABLE 3. Area by season interaction effects on mean standing-crop sporocarp biomass (g/ha dry weight) (± 1 SE) in two study areas at Watson Falls and for the two seasons sampled, fall 1993 and spring 1994. Fungal groups that do not share a superscript letter across areas and seasons are significantly different by Fisher's Protected LSD test ($p \leq 0.1$) based on transformed data; n = 3.

Fungal Group	Airstrip				Mowich			
	Fall		Spring		Fall		Spring	
Mushrooms								
Boletaceae	89^{a}	(48)	10^{b}	(6)	10^{b}	(8)	106^{a}	(40)
Cortinariaceae	23^{a}	(12)	33^{a}	(3)	50^{a}	(23)	163^{b}	(23)
Total mushrooms	503^{a}	(95)	111^{b}	(43)	666^{a}	(191)	749^{a}	(266)
Truffles								
Gautieria	133^{ab}	(100)	883^{a}	(286)	20^{b}	(20)	4537^{c}	(2294)
Other truffles	80^{a}	(80)	79^{a}	(26)	57^{a}	(57)	2156^{b}	(1054)
Total truffles	3030^{a}	(2079)	2280^{a}	(571)	2440^{a}	(657)	9780^{b}	(3410)

TABLE 4. Mean frequency (%) (± 1 SE) of truffle spores or plant fragments in fecal pellets from western red-backed voles, northern flying squirrels, and Siskiyou chipmunks at Watson Falls, fall 1993; n=6.

Food Item	Frequency (± 1 SE)[1]	
Truffles		
Gautieria	37.3[a]	(4.8)
Hysterangium	21.4[a]	(4.4)
Leucogaster	14.5[b]	(3.4)
Rhizopogon/Truncocolumella	99.7[c]	(0.3)
Plant material	63.1[d]	(2.3)

[1]Food item frequency values that do not share a superscript letter are significantly different by Fisher's Protected LSD test ($p \leq 0.1$).

The importance of other fungal genera varied in the diets of small mammals. Northern flying squirrels had a significantly ($p \leq 0.1$) higher frequency of *Gautieria* spores in fecal pellets than did western red-backed voles or Siskiyou chipmunks (Table 5). Western red-backed voles had a significantly ($p \leq 0.02$) lower frequency of *Leucogaster* spores in fecal pellets than did Siskiyou chipmunks (Table 5). Significant area-by-animal interactions were found for *Hysterangium* and plant material (Table 6). *Gautieria* spores were more frequent in fecal pellets from the Mowich area and *Hysterangium* spores from the Airstrip area (Table 5).

For the three most frequent truffles as a group, the correlation between truffle standing crop and truffle dietary frequency was significant for all three mammal species (Table 7). Individually, however, none of the major truffle genera showed strong correlations between frequency of spore occurrence in fecal pellets and sporocarp biomass within a treatment unit (Table 7). Total truffle standing crop within a unit did not correlate significantly with the frequency of plant material in the diets of the three mammal species, however there was an inverse correlation for western red-backed voles (rho = -0.60, $p = 0.18$).

Spring

In spring 1994, *Gautieria*, *Hysterangium*, *Leucogaster,* and *Rhizopogon* (*Truncocolumella* does not fruit in spring) were major food items in the diet of northern flying squirrels, the only animal examined that season. No differences in the frequencies of truffle spores in fecal pellets were observed between the Airstrip and Mowich areas (Table 8). The frequencies of *Gautieria* and *Hysterangium* spores were higher in spring than in fall for northern flying squirrels (Tables 5 and 8). The Mowich area had lower *Rhizopogon/Truncocolumella* spore frequency in spring than fall (Tables 5 and 8).

For the four major spring food items as a group and individually, no strong correlation between truffle standing crop and spore frequencies were found (Table 9). For northern flying squirrels, the dietary frequency of plant material was negatively correlated with *Rhizopogon* sporocarp biomass ($r = -0.75$, $p = 0.08$).

Small Mammal Abundance

Western red-backed voles were most abundant (fall only) followed by Siskiyou chipmunks and northern flying squirrels ($p \leq 0.05$). Siskiyou chipmunks were more abundant in the Mowich area than the Airstrip area (Table 10).

TABLE 5. Mean frequency (%) (± 1 SE) of truffle spores or plant fragments in fecal pellets from three mammal species and ANOVA results in two study areas at Watson Falls, fall 1993. Food item values that do not share a superscript letter among animals are significantly different by Fisher's Protected LSD test ($p \leq 0.1$) based on transformed data.

	Area (n = 18)			Animal (n = 12)			
Food Item	Airstrip	Mowich	*p*	western red-backed vole	northern flying squirrel	Siskiyou chipmunk	*p*
Truffles							
Gautieria	21.6 (5.2)	59.9 (7.1)	0.0004	33.0[a] (5.2)	64.7[b] (15.0)	28.3[a] (10.9)	0.15
Hysterangium[1]	28.8 (6.3)	10.7 (5.4)	0.02	22.3 (5.7)	20.9 (10.9)	18.8 (9.7)	0.47
Leucogaster	10.5 (3.2)	20.3 (6.7)	0.51	3.4[a] (1.3)	27.2[ab] (10.7)	39.7[b] (10.5)	0.02
Rhizopogon/ Truncocolumella	100.0 (0.0)	99.1 (0.7)	0.15	99.9 (0.1)	100.0 (0.0)	98.7 (1.3)	0.54
Plant material[1]	58.4 (3.2)	69.8 (2.6)	0.0006	63.6 (1.6)	51.7 (11.3)	70.7 (3.5)	0.08

[1] Significant area by animal interaction precludes simple main effects comparisons. See Table 6 for detailed interaction effects.

TABLE 6. Area by animal interaction effects on the mean frequency (%) (± 1 SE) of *Hysterangium* spores or plant fragments in fecal pellets from three small mammal species in two study locations at Watson Falls, fall 1993. Values that do not share a superscript letter across areas and animals are significantly different by Fisher's Protected LSD test ($p \leq 0.1$) based on transformed data; n = 6.

	Airstrip						Mowich					
Food Item	western red-backed vole		northern flying squirrel		Siskiyou chipmunk		western red-backed vole		northern flying squirrel		Siskiyou chipmunk	
Hysterangium	33.4[a]	(7.7)	37.0[a]	(21.9)	3.0[b]	(1.5)	0.0[b]	(0.0)	10.2[b]	(10.2)	34.7[a]	(17.6)
Plant material	63.1[a]	(2.2)	20.5[b]	(15.1)	66.3[a]	(4.2)	64.7[a]	(2.0)	72.6[ac]	(8.4)	78.0[c]	(3.6)

TABLE 7. Spearman rank correlation, rho, between truffle standing-crop biomass and mean frequency of truffle spores in fecal pellets, ranked by treatment unit (n = 6) of the Watson Falls block, fall 1993; *p* values in parentheses.

	Animal					
Food Item	western red-backed vole		northern flying squirrel		Siskiyou chipmunk	
Gautieria	0.58	(0.20)	0.65	(0.15)	-0.28	(0.54)
Hysterangium	-0.34	(0.43)	-0.36	(0.43)	-0.09	(0.84)
Rhizopogon/Truncocolumella	0.13	(0.77)	0.50	(0.26)	-0.66	(0.14)
Pooled items	0.70	(0.004)	0.66	(0.007)	0.64	(0.008)

TABLE 8. Mean frequency (%) (±1 SE) of truffle spores or plant fragments in northern flying squirrel fecal pellets and ANOVA results from two study areas at Watson Falls, spring 1994. Whole block food items that do not share a superscript letter are significantly different by Fisher's Protected LSD test ($p \leq 0.1$) based on transformed data.

	Area (n =3)			Whole block
Food Item	Airstrip	Mowich	*p*	(n=6)
Truffles				
Gautieria	91.9 (8.1)	96.5 (3.4)	0.79	94.2[a] (4.1)
Hysterangium	87.1 (4.3)	56.7 (22.5)	0.73	71.9[b](12.3)
Leucogaster	10.9 (6.4)	9.7 (5.5)	0.85	10.3[c] (3.8)
Rhizopogon	99.3 (0.7)	84.8 (10.1)	0.26	92.0[a] (5.6)
Plant material	7.3 (2.6)	29.0 (12.2)	0.16	18.2[c] (7.4)

TABLE 9. Spearman rank correlation, rho, between truffle standing-crop biomass and mean frequency of truffle spores in fecal pellets of northern flying squirrels, ranked by treatment unit (n = 6) of the Watson Falls block, spring 1994; *p* values in parentheses.

Food Item	rho	(*p*)
Gautieria	0.09	(0.84)
Hysterangium	-0.38	(0.41)
Leucogaster	-0.64	(0.15)
Rhizopogon	0.52	(0.25)
Pooled items	0.23	(0.26)

Discussion

Sporocarp Abundance

Our results suggest that there are potentially large differences in the distribution and abundance of fungal sporocarps among our study sites, but that these differences may be apparent only during particular seasons. Truffles in particular showed strong seasonal effects. For example, the prolific spring fruiting of *Gautieria* and other minor truffle species at Mowich produced standing crops three to four times greater than those observed in the same locations in fall or in either season at the Airstrip sites. Similar seasonal variation in truffle production has been noted at the H. J. Andrews Experimental Forest, 100 km to the north of Watson Falls (Luoma 1991).

Truffle biomass greatly exceeded mushroom biomass during both sample periods. Similarly, in a study of 15 Douglas-fir stands from southwestern Oregon, truffle species were seven of the ten most abundant producers of sporocarps (D. L. Luoma, unpubl. data). These below-ground fruiting fungi are insulated from desiccation and freezing effects that can prevent mushrooms from reaching spore maturation. Although fall is generally

TABLE 10. Number of captures per 100 trap nights (± 1 SE) of three mammal species in the two study locations at Watson Falls, and for the two seasons sampled, fall 1993 and spring 1994; n = 6 except n = 3 for the Airstrip vs. Mowich comparison of western red-backed voles.

Animal	Area					Season				
	Airstrip		Mowich		p[1]	Fall		Spring		p
western red-backed vole	5.0	(2.1)	3.1	(0.7)	0.23	4.1	(0.8)	ND[2]		—
northern flying squirrel	0.5	(0.2)	0.8	(0.3)	0.37	0.9	(0.3)	0.3	(0.1)	0.23
Siskiyou chipmunk	1.5	(0.1)	3.9	(0.7)	0.005	2.2	(0.5)	3.2	(0.9)	0.21

[1]p values from two-way ANOVA based on transformed data.
[2]ND = No data.

when mushroom production is greatest (Fogel and Hunt 1979; North et al. 1997; D. L. Luoma, unpubl. data), fall mushroom biomass was low in this study. In subsequent years, mushroom biomass on the Watson Falls block was 8-10 times greater than in fall 1993 (D. L. Luoma, unpubl. data). We hypothesize that weather patterns are largely responsible for the low mushroom production in 1993. Unusually droughty conditions persisted from late August through mid-October that year.

Generally in our region, annual and seasonal truffle production are less variable than mushroom production (North et al. 1997; D. L. Luoma, unpubl. data). Truffles also fruit over a longer period of time (Fogel and Hunt 1979, North et al. 1997). For example, at one 3-ha ponderosa pine site in southwest Oregon, truffles have been found every week of the year (J. M. Trappe, unpubl. data). Both the seasonally-extended availability and greater biomass of truffles increase their dependability as a food source for small mammals.

Mycophagy

Our finding that northern flying squirrels consumed *Gautieria* more frequently than did western red-backed voles or Siskiyou chipmunks provides field-based support for a similar pattern observed by Zabel and Waters (1997) who found that flying squirrels preferred *Gautieria* in "cafeteria-style" feeding trials. Their study did not include *Rhizopogon*, which we found to be nearly ubiquitous in fecal pellets and which had the greatest sporocarp standing crop during fall 1993. *Rhizopogon* and *Gautieria* sporocarps may be particularly important food sources in these forests.

That all three small mammal species consumed *Gautieria* less frequently in the Airstrip units is not easily explained by variation in standing crop alone, which if anything, was slightly higher in the Airstrip units during fall. The significantly higher number of Siskiyou chipmunks in the Mowich units could have increased predation rates on *Gautieria* in that area and thereby lowered standing-crop biomass. Spatial patterns of consumption may be a consequence of interactions between sporocarp availability, small mammal abundance, and food item preferences leading to complex competitive effects among small mammal species that vary spatially and temporally.

In the fall, the biomass of ectomycorrhizal mushrooms equaled or exceeded that of the truffle genera *Gautieria* and *Hysterangium*. Yet, despite the comparable abundance of mushroom sporocarps, truffle genera were significantly more frequent in the diets of all three small mammal species. This suggests that truffles are a preferred food in these Douglas-fir stands. No spores of the mushroom groups Russulaceae or Aphyllophorales were found in the diet analysis of any of the three small mammal species even though their sporocarp biomass exceeded that of all truffle genera except for *Rhizopogon/Truncocolumella*. Thus, EM mushrooms do not appear to be a dietary staple for these small mammal species in the Watson Falls block.

Both *Gautieria* and *Hysterangium* appear to be consumed, to some extent, in proportion the their seasonal abundance. In contrast, although *Rhizopogon/Truncocolumella* biomass decreased sharply in the spring, it remained an important component of the diet of flying squirrels. The results of other research and our own observations lead us to speculate that *Gautieria* and *Rhizopogon* may be equally preferred as food by northern flying squirrels. When maintenance of small mammal abundance and diversity are goals, management that maintains sporocarp production by truffle fungi may be crucial for success.

Dietary Correlations

In our study, the positive correlation between frequency of *Gautieria* spores in northern flying squirrel fecal pellets and *Gautieria* biomass lends further support to the hypothesis that northern flying squirrels have a preference for this genus. Colgan (1997) found that despite the reduced fruiting of *Gautieria* in thinned stands, flying squirrels trapped in those stands were continuing to utilize *Gautieria* as a dominant food source. He hypothesized that flying squirrel preference for *Gautieria* could further reduce standing crop biomass in those stands (beyond that induced by the thinning) forcing flying squirrels to obtain *Gautieria* outside the thinned treatment areas. The much larger, contiguous treatment areas of the DEMO experiment will reduce the influence of this type of edge effect.

The significant correlation between truffle standing-crop biomass and frequency of truffle spores in fecal pellets for the pooled food items must be view with some caution. The correlation was mainly the result of a few high *Rhizopogon/ Truncocolumella* sporocarp biomass values coinciding with high dietary frequency values while *Gautieria* and *Hysterangium* tended to have lower biomass and spore frequency values. As an individual food item, there is no correlation between truffle standing-crop biomass and frequency of truffle spores in fecal pellets for *Rhizopogon/ Truncocolumella* because these are eaten ubiquitously, regardless of variation in peak-season standing-crop biomass.

Negative correlations between the Siskiyou chipmunk and *Gautieria* may indicate that increased competition for truffles reduces sporocarp standing-crop biomass. North et al. (1997) have demonstrated predation effects on truffle standing crop in northwestern Washington. In spring, the negative correlation between fungal biomass and spores of *Leucogaster* in the diet (Table 8) again suggests that mycophagy may affect sporocarp standing-crop biomass. When truffle biomass is lowered, consumption of plant material may increase, however unexplored complexities involving animal abundance, competitive ability, and food preference limit our ability to generalize from this study.

Small Mammal Abundance

Truffle abundance probably has an important influence on the abundance of mycophagous small mammals. In addition to higher Siskiyou chipmunk abundance at Mowich in fall, were higher *Gautieria* consumption by all three animals studied and reduced *Gautieria* standing-crop biomass. However, factors other than truffle abundance could also affect the densities of small mammal species in these stands. Variation in tree basal area, snags, downed trees, and tree cavities may influence the availability of cover, food, and nesting areas (Gilbert and Allwine 1991). The movements of animals from adjacent stands and variation in local predation rates can also influence small mammal abundance (Carey 1991, Lehmkuhl and Ruggiero 1991). These potential effects were not analyzed in the current study but will be considered by other researchers in subsequent analyses of wildlife patterns (Lehmkuhl et al. 1998). Further exploration of the sources of between-area differences will be an important part of our baseline, pre-harvest analysis; the patterns and causes of these differences will be of fundamental importance to understanding variation in the relationships that emerge following imposition of the DEMO harvest treatments.

Conclusions

We identified significant spatial and temporal variation in EMF production, small mammal mycophagy, and small mammal abundance in the pre-harvest forests of the Watson Falls block. However, truffles were consistently the primary food item in the diet of all three small mammal species studied. Small mammals are potentially important dispersal agents of truffles into disturbed areas where EMF are locally extirpated. Although this study represents only a "snap shot" in time, future analyses will examine responses to various levels and patterns of green-tree retention over multiple years, thus broadening the scope of inference for our findings.

Northern flying squirrels and Siskiyou chipmunks nest in trees or use trees as avenues for travel (Carey 1991). Arboreal rodents may be affected by forest management activities that change the pattern and structure of forest canopies. Trees also provide the energy sources for EMF and their fruiting bodies. Therefore, disturbances that influence the level and pattern of live trees retained through harvest are also likely to influence the diversity, abundance, and distribution of EMF and their fruiting bodies. Future analyses of post-harvest patterns will provide

valuable insights into the effects of retention harvest on EMF and small mammal abundance. Given the functional importance of these groups in our forest ecosystems, the results of our work will have important implications for how retention harvests may be implemented in the future.

Acknowledgements

We gratefully acknowledge the contributions of Jim Caruthers, Wanda Caruthers, Joyce Eberhart, Dr. Laura D. de Toledo, Rick Abbott, Debbie Claridge, Jeff Feen, Dr. Ari Jumpponen, Kim Kittridge, Tom Manning, Dr. Bill McComb, and Rebecca Thompson. Dr. Charlie Halpern's guidance was especially helpful in developing this contribution to a Special Issue of Northwest Science. Drs. Andrew Claridge, Chris Maguire, Malcolm North, Tim Schowalter, and Cindy Zabel provided many helpful comments.

This is a product of the Demonstration of Ecosystem Management Options (DEMO) study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources.

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Arboreal Invertebrate Responses to Varying Levels and Patterns of Green-tree Retention in Northwestern Forests

Abstract

Canopy arthropods play an important role in forest ecosystems and are sensitive to anthropogenic disturbances. The DEMO (Demonstration of Ecosystem Management Options) study investigates the influence of varying levels and patterns of green-tree retention on diverse elements of northwestern forest ecosystems. In this paper we review the literature on forest management effects on canopy arthropods and describe research in progress on the response of arboreal arthropod communities to retention harvests in the Pacific Northwest. Pre-treatment foliage was pruned and canopy arthropods collected from dominant overstory and understory vegetation within six treatment units in eight experimental blocks in western Oregon and Washington. Significant pre-treatment differences in abundance were found among blocks and treatments for several taxa in the overstory. Block-level differences reflect natural variation in the geographic distribution of arthropod taxa. Differences among treatment units may reflect the influence of local variation. Following harvest treatments, we expect to see changes in arthropod richness, abundance and functional group organization in dominant overstory and understory canopies reflecting the influence of magnitude and pattern of green-tree retention.

Introduction

Recent public concern has led to changes in management objectives for forests of the Pacific Northwest. The concerns for managed forests focus on maintaining or restoring many of the ecological structures and functions found in natural forest ecosystems. The current challenge is to provide silvicultural prescriptions for regeneration harvests that provide a sustainable rate of timber harvesting while maintaining many of the structures and functions characteristic of late-successional forests. New management objectives have resulted in regeneration harvest prescriptions for preserving or creating snags, down woody debris, and green trees in riparian reserves and upland stands (Tappeiner et al. 1991). However, it is unknown how successful regeneration harvests will be in meeting management objectives.

The Demonstration of Ecosystem Management Options (DEMO) study is designed to provide information for developing new silvicultural strategies to retain some of the key ecological features of unmanaged forests by using regeneration harvests in forests dominated by medium- and large-sized conifers. The DEMO study is comprised of eight geographic locations (blocks) with a replicated, random application of six treatments applied to 13 ha (32 acre) stands, representing different levels of evenly dispersed, or aggregated tree retention (Aubry et al. 1999). Treatments include a control (no harvest); 75% retention, with the trees harvested in three, one-ha circular patches (gaps); 40 and 15% aggregated retention of five and two, one-ha circular forest patches (or fragments), respectively; and 40 and 15% retention, evenly distributed (thinned).

Canopy arthropod faunas are important components of forest ecosystems. They include economically important "pests", biological control agents (Schowalter 1995, Winchester 1997), and phytophagous insects that are part of the food web. Canopy invertebrates affect plant species composition, leaf area and canopy-atmosphere interactions, as well as water and nutrient fluxes to the forest floor (Seastedt and Crossley 1984; Schowalter et al. 1986, 1991; Schowalter and Sabin 1991). Hence, responses of canopy communities to forest management practices are particularly critical to ecosystem function and forest health. Forest management practices are known to affect overall invertebrate diversity and the propensity for pest outbreaks (e.g., Kareiva 1983, McMillin and Wagner 1993, Schowalter and Turchin 1993, Pettersson et al. 1995). Reduction of host tree density should have strong effects on herbivore populations due to changes in microclimate, host condition, and the proximity of new hosts (Lorio 1980, Schowalter et al. 1986, Amman

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et al. 1988, McMillin and Wagner 1993). Many predators and detritivores as well as some herbivores are less abundant or absent in disturbed stands (Kruess and Tscharntke 1994, Schowalter 1994, 1995).

In this paper we review the literature on the effects of silvicultural practices on the response of arthropod communities. We pose a set of hypothesized responses to the DEMO treatments, discuss the rationale for the sampling method used, describe the communities of interest, and provide a pre-harvest analysis of the arthropod groups showing sufficient abundance.

Statistical comparison of arthropod abundances, community structure (e.g., proportional representation of functional guilds), and diversity indices among the replicated treatments will indicate the degree and pattern of canopy openness necessary to elicit responses of various taxa. We will evaluate the extent to which varying levels of green-tree retention maintain populations of species characteristic of uncut forest and provide habitat for species characteristic of regenerating canopies.

The varied levels and spatial patterns of tree retention tested in the DEMO study should have strong effects on the arthropod community. Defoliators may increase or decrease in abundance, depending on the species. As the understory responds to the increased availability of light, water, and nutrients, species associated with shrubs and forbs should increase in richness and abundance. The aggregated retention treatments should have relatively minor short-term effects on canopy arthropods in the interior of the forest remnants. However, fragmentation and edge effects should influence species distribution, abundance and richness. Therefore, we pose the following hypotheses:

(1) As levels of retention decrease, the abundance of sap-sucking insects will increase, and defoliators, bark beetles, and predators will decrease in the overstory.

(2) The diversity and abundance of arthropods in the understory will vary inversely with the level of retention.

(3) The abundance and richness of flightless species, predators and parasitoids will vary proportionally with the degree of green-tree retention.

(4) The magnitude of change in arthropod abundance and community structure will increase as follows: control < 75% aggregated < 40% aggregated < 15% aggregated < 40% dispersed < 15% dispersed.

Canopy Arthropod Responses to Changes in Forest Structure

Arthropod responses to varying levels and patterns of green-tree retention will reflect the differential dispersal abilities of canopy taxa (especially flightless species) in addition to differential sensitivity to altered microclimate and foliage quality. Previous studies have shown that tree harvest may elicit responses in arthropod fauna at the stand-level (Schowalter 1988, 1995; Shure and Phillips 1991).

Some pest invertebrate species are likely to increase in abundance in response to green-tree retention harvest. For example, in plantations, tree mortality caused by insect-vectored blackstain root disease (*Leptographium wageneri*) is aggravated by the proximity of breeding sites in the remaining stumps and slash in partially harvested stands (e.g., Witcosky et al. 1986). Spruce budworm (*Choristoneura fumiferana*) reared on trees in a newly thinned stand developed faster and removed 43% more foliage than in an unthinned stand (Bauce 1996). The white pine weevil (*Pissodes strὸbi*) and several species of tip moths are more abundant and injurious in open-grown saplings compared to densely stocked trees (Furniss and Carolin 1977). Reduced predator diversity or abundance may contribute to their outbreaks.

Other pest species are likely to decline in abundance as a result of a reduction in tree density. Increasing tree spacing to > 6 m (20 ft) can prevent outbreaks of several bark beetle species (Sartwell and Stevens 1976, Mitchell et al. 1983, Nebeker et al. 1985, Brown et al. 1987, Schowalter and Turchin 1993). Some defoliators are also sensitive to tree spacing and show reduced abundances in thinned stands (Batzer 1976, Lance 1983, Schowalter 1995).

Understory growth is stimulated after partial harvest by the increased availability of light, water and nutrients (Walker et al. 1986, Tappeiner and Alaback 1990) . Hence, those arthropods associated with understory plants should also change in abundance and composition. However, these responses may vary depending on changes in host plant condition. Although difficult to predict on

an individual basis, populations of herbivorous species generally increase as host density and biomass increase. Evaluating trends in arthropod populations associated with understory plant species may be important in understanding changes in diversity and dynamics of the communities.

Creation of small, isolated aggregates (fragments) of forest through partial harvest are likely to have negative impacts on arthropod communities. Biotic communities are affected by altered microclimate, isolation from potential habitat, and fragment shape (Saunders et al. 1991, Didham et al. 1996). Although little information exists on the effect of fragmentation on arthropods, some studies indicate that fragmentation results in a loss of species richness (Kruess and Tscharntke 1994, Turner 1996). In tropical forests, fragmentation directly affects pollination through a reduction in the abundance and diversity of pollinators, and indirectly by the alteration of flight patterns and pollinator behavior (Powell and Powell 1987). Natural enemies of phytophagous insects are at greater risk of extinction or decline following disturbance than are their insect prey (Kruess and Tscharntke 1994; Schowalter 1994, 1995). For example, Kareiva (1987) found that habitat fragmentation indirectly promoted aphid outbreaks through its influence on predaceous *Cocinella* foraging behavior. Other effects of fragmentation include changes in species composition. Punttila et al. (1994) found unique ant communities in old-growth forest and adjacent clearcuts, indicating functional guild constancy, but altered species composition. Klein (1989) showed that the dung beetle community is increasingly altered with decreasing fragment size; there is little evidence of movement of forest dung beetles across clearcuts to other forest fragments, resulting in isolation.

One of the most consequential effects of forest fragmentation is the creation of abrupt edge zones (Chen et al. 1992, Murcia 1995). Forest edges are characterized by gradients of air and soil temperature, relative humidity, short-wave radiation, and wind speed, that may extend 100 to more than 200 m into the interior of the fragment or forest (Chen et al. 1995). Studies of vertebrates suggest that the penetration of edge effects varies with the taxon and region (Ozanne et al. 1997). Edge has been shown to be a barrier to movement of some detritivores, parasitoids, predators and ground beetles (Kareiva 1987, Klein 1989, Kruess and Tscharntke 1994, Punttila et al. 1994, Roland and Kaupp 1995) and to affect species distributions (Murcia 1995). Malcolm (1997) found that total insect biomass increased in the understory and decreased in the overstory of fragmented forests as a result of edge effects. Ozanne et al. (1997) noted that overall arthropod abundance and biomass dropped significantly near the forest edge.

The lowered humidity and higher wind speeds associated with edge habitat are most likely to affect smaller organisms with a high surface-to volume ratio (Ozanne et al. 1997). Psocoptera and Collembola, which primarily feed on fungi and algae on the surfaces of needles and bark are known to require high humidity (Broadhead and Thornton 1955, Bowden et al. 1976). Conversely, on Norway spruce (*Picea abies*), Thysanoptera, which are tolerant of dry, open environments, were higher in abundance at the edge than toward the fragment core (Ozanne et al. 1997). Homoptera, on Scots pine (*Pinus sylvestris*), were also higher in abundance at the forest edge, and likely reflect responses to increased foliage density on edge trees (Ranney et al. 1981, Denno and Roderick 1991).

Fragmentation also affects arthropod vulnerability to parasites and disease organisms. A reduced infection of a forest damselfly by a zygopteran gregarine parasite (that attaches to leg bristles of the host) was noted by Taylor and Merriam (1996). Forest fragmentation increased damselfly foraging away from streams (in search of alternate prey), thus decreasing exposure to the parasite. Outbreaks of forest tent caterpillars (*Malacosoma disstria*) can be prolonged by habitat fragmentation due to reduced transmission of nuclear polyhedrosis virus and declines in natural enemies (Roland 1993, Roland and Kaupp 1995).

Study Areas

Eight study sites (blocks) representing a range of physical environments, stand ages, and forest structures were selected in western Oregon and Washington to establish a broad ecological and geographical foundation of inference. Each of the blocks was selected to minimize variation in physiographic and stand characteristics among the six treatments within each block (Aubry et al.

1999). Elevation ranges from 200-1700 m, inclination varies from gentle to steep, and nearly all slope aspects are represented (see Table 1 in Aubry et al. [1999]). The harvest histories vary: three blocks (Little White Salmon, Paradise Hills, and Butte) on the Gifford Pinchot N. F. represent natural, uncut forest. All blocks on the Umpqua N. F. have experienced some degree of thinning or salvage logging; two blocks (Layng Creek, Oregon and Capitol Forest, Washington) support second-growth stands.

This range of physiographic and stand conditions significantly contribute to the environmental diversity among blocks. The understories are compositionally diverse. For example, some blocks have dense herb and shrub communities, while others support sparse ground layers. Many blocks, however, share the same woody and herbaceous understory dominants (e.g., *Acer circinatum*, *Berberis nervosa*, *Gaultheria shallon*, *Vaccinium* spp., *Tsuga heterophylla*) (Halpern et al. 1999).

Component Communities for Sampling

Selection of plant species for sampling was based on their expected contribution to invertebrate community structure. Within a site, invertebrate communities can be partitioned into component communities (Moore and Hunt 1988). Component communities are relatively distinct, overlapping assemblages that reflect the biochemical or behavioral adaptation of most invertebrates and their host-specific predators and parasites to specific resources.

Within a stand, two major component communities are found in the forest overstory and understory, two layers of vegetation that partition invertebrates based on their tolerances of temperature and moisture and on their preferences for particular stages of plant growth. Hence, component communities within conifer saplings and the upper crowns of dominant trees are more similar to each other than to the component community of the moist, shaded mid-crown (Parker 1995, Schowalter 1995). This study examines changes in these vertically-defined communities.

Component communities are further delineated by associations with host plants. Some host plants contribute more to invertebrate community structure than do others. Overstory Douglas-fir clearly contributes to the invertebrate community in our pre-treatment DEMO forests, as (eventually) will Douglas-fir saplings in large openings. Major understory plant species, including western hemlock (*Tsuga heterophylla*), vine maple (*Acer circinatum*), and huckleberries (*Vaccinium* spp.), substantially contribute to understory arthropod communities. By sampling arthropods associated with these species, we should capture the responses of the key invertebrate communities to the DEMO treatments.

Sampling Methods

We employ a standard bagging technique to sample the resident canopy fauna. Vegetation sampling techniques provide quantitative estimates of population sizes for species associated with particular plant species, rather than the simple estimates of relative population densities provided by fogging or by interception of flying insects. The foliage bagging technique emphasizes resident fauna, those species closely associated with the plant, and it samples important herbivores such as sessile and leaf-mining species that are missed by fogging or other techniques designed to trap flying insects (Majer and Recher 1988, Schowalter 1989, Blanton 1990). The major conifer-defoliating insect species typically concentrate feeding along portions of branchlets. Hence, herbivory can be estimated by measuring the length of branchlets exhibiting chewed needles (Schowalter 1995).

Bagging permits standardization of invertebrate population size on a per gram foliage basis. These data, together with data on host plant density or biomass, permit calculation of invertebrate population density, i.e., numbers or biomass per hectare (Schowalter 1995). Such data not only provide information on the magnitude of change in invertebrate populations due to treatments, but also provide information on population density necessary to evaluate population viability (e.g., by indicating proximity of individuals relative to thresholds for attraction of mates). On the other hand, bagging does not capture overall species diversity because some active species may be disturbed during sampling and some important species (such as bark beetles) are more efficiently collected in flight interception traps or by sampling dead and dying trees.

One overstory Douglas-fir in each replicate of each canopy retention treatment unit (24 trees each

in Oregon and Washington) was rigged with pulleys and ropes in 1996 to provide non-injurious future canopy access (e.g., Schowalter 1989, 1995). Given the degree of treatment replication by blocks in this study, sampling one tree per replicate stand is sufficient for treatment comparison. Sampling of additional trees in each replicate stand would provide a better stand-level mean for ANOVA, reducing the influence of outlier units and reduce spurious treatment effects. However, additional trees provide no additional degrees of freedom for statistical comparison of treatment effects (Hurlbert 1984), and the additional time and cost of sampling extra trees is prohibitive. We assume that arthropod variation is greater across the landscape than within individual stands. If this assumption is invalid, then arthropod variation among stands should mask any treatment effect. Previous studies (Schowalter 1989, 1994, 1995) consistently showed significant responses to harvest and environmental disturbance by the same arthropod groups.

After harvest of several of the Washington treatment blocks in 1998, a tree near the edge and in the center of the aggregated treatment stands will be sampled to test for edge and fragmentation effects. Additionally, the gap treatment (75% aggregated) will be sampled with a tree near the edge, and a tree 100 m into the uncut matrix.

Samples are being collected at upper, middle and lower canopy levels of each tree in June and August to represent vertical stratification of the relatively distinct spring and summer faunas (Schowalter 1995). One foliage-bearing branch (about 50 cm in length or 30-50 g plant mass) at each canopy level is enclosed quickly in a plastic bag, clipped from the tree, and the bag sealed (Schowalter 1995). Invertebrates are sorted to the lowest possible taxonomic level. Branches are examined for evidence of herbivory and dried to constant weight. Invertebrate abundances are expressed as number per kg of plant mass.

All eight replicates of the six treatments were used to compare the pre-treatment abundances of overstory and understory invertebrates. This permits statistical comparison of population size, indices of community structure, and species diversity among treatments using a randomized, complete-block experimental design (Steel and Torrie 1980).

Analysis and Interpretation of a Subset of Pre-treatment Patterns

We now have two years of pre-treatment data that permit assessment of similarity among plots in the Oregon and Washington study blocks. Pre-treatment sampling has established the baseline from which to evaluate the future changes in invertebrate abundances and diversity resulting from the retention treatments. Three years of post-treatment sampling will reveal short-term effects of treatments on population sizes and diversity.

Invertebrate abundances (number/kg plant sample) from Douglas-fir for 1996 were pooled for each tree by canopy level and season to represent the entire arthropod community and to have sufficient abundances for analysis. The distribution of each taxon was examined for normality and the data were transformed ($\sqrt{[y+0.5]}$) to better meet assumptions of normality for ANOVA (Sokal and Rohlf 1981). However, pooling and transformation were ineffective in normalizing all taxa analyzed due to insufficient abundances in some treatment units (Table 1). All analyses were conducted using JMP software (SAS Inst. Inc. 1986).

Within the overstory canopy community, 94 taxonomic groups were collected in 1996. Of these, 22 were analyzed by ANOVA (Table 1). Significant differences ($p< 0.05$) among blocks were observed in the budmoth (*Zeiraphera hesperiana* Mutuura and Freeman), the sap-feeder functional group, and *Nuculaspis californica* (Coleman) scales (all higher in Layng Creek, Oregon); *Straminaspis kelloggi* (Coleman) scales (higher in Layng Creek and Little White Salmon, Washington); *Chionaspis pinafoliae* (Fitch) scales (higher in Layng Creek than all other blocks excluding Little White Salmon, Washington); the predator functional group (lower in Dog Prairie, Oregon); syrphid larvae (higher in Butte and Capitol Forest, Washington); hypogasturid Collémbola (higher in Capitol Forest); *Scapheremaeus* sp. oribatids (higher in Layng Creek); *Camisia carrolli* Andre oribatids (lower in Little River and Dog Prairie, Oregon); Psocoptera (lower in Dog Prairie than Layng Creek and Watson Falls, Oregon, and Capitol and Butte Forests, Washington, and Little River lower than Layng Creek, Oregon); and small and large *Jugatala* spp. (higher in Paradise Hills and Dog Prairie, respectively). Some of the significant block effects are attributed to

TABLE 1. Pre-treatment means (±1 SE), and analysis of variance results for 22 canopy arthropod taxa and functional guilds (in overstory Douglas-fir). Only those groups that exhibited sufficient abundance were analyzed individually. Functional guilds include taxa that were not sufficiently abundant to be analyzed individually. Treatments are: (1) 100% retention, (2) 75% retention (gaps), (3) 40% retention (dispersed), (4) 40% retention (aggregated), (5) 15% retention (dispersed), and (6) 15% retention (aggregated). Analyses were performed on transformed data ($\sqrt{[y+0.5]}$). Treatment means and SEs are untransformed values. There were 5 df for treatment and 7 for block. * = significant at p 0.05.

	Treatment mean (± 1 SE)								Significance (P)	
Taxon	1	2	3	4	5	6	MSE	Treatment F	Treatment	Block
Defoliators	6.8	1.8	3.5	6.5	2.2	3.0	1.57	0.62	0.68	0.71
	(2.89)	(1.13)	(1.40)	(3.55)	(0.67)	(1.24)				
Zeiraphera hesperiana	0.57	1.22	0.00	0.00	0.00	1.08	0.25	0.94	0.46	0.01*
	(0.57)	(0.82)	(0.00)	(0.00)	(0.00)	(1.08)				
Geometridae	4.74	0.37	1.87	3.14	0.33	0.33	0.80	2.06	0.09	0.70
	(1.89)	(0.37)	(1.23)	(2.14)	(0.33)	(0.33)				
Diprionidae	0.00	0.00	0.95	3.31	0.91	0.00	0.55	0.84	0.53	0.24
	(0.00)	(0.00)	(0.65)	(3.31)	(0.60)	(0.00)				
Sap feeders	111.38	39.76	30.54	51.91	71.83	117.32	19.81	0.86	0.51	0.01*
	(53.10)	(13.64)	(7.97)	(11.35)	(25.81)	(59.53)				
Phlaeothrípidae	1.09	1.15	2.28	0.99	3.64	0.31	0.76	0.55	0.73	0.09
	(0.55)	(0.56)	(1.49)	(0.67)	(2.99)	(0.31)				
Nuculaspis californica	17.87	3.73	0.36	4.85	0.57	32.43	8.80	0.45	0.80	0.01*
	(17.87)	(3.73)	(0.36)	(4.85)	(0.57)	(32.43)				
Chionaspis pinifoliae	0.57	2.24	0.00	2.23	0.66	26.82	3.90	1.66	0.16	0.04*
	(0.57)	(2.24)	(0.00)	(1.48)	(0.69)	(20.90)				
Adelges cooleyi	9.07	15.20	6.40	11.95	9.61	11.39	4.13	0.44	0.82	0.40
	(5.10)	(7.57)	(2.24)	(4.99)	(7.64)	(4.55)				
Straminaspis kelloggi	24.90	0.98	0.78	3.57	0.00	18.93	5.73	1.49	0.21	0.01*
	(17.23)	(0.67)	(0.53)	(3.57)	(0.00)	(11.66)				
Cinara sp.	8.37	3.09	1.65	6.05	12.35	2.85	3.04	1.12	0.36	0.23
	(6.14)	(1.55)	(1.19)	(4.74)	(4.86)	(2.85)				
Pseudocóccidae	6.22	0.25	0.00	0.60	0.89	1.75	0.90	1.54	0.19	0.24
	(4.34)	(0.25)	(0.00)	(0.60)	(0.59)	(1.25)				
Seed feeders	0.00	0.00	0.30	0.00	0.74	0.31	0.11	0.65	0.66	0.11
	(0.00)	(0.00)	(0.30)	(0.00)	(0.74)	(0.31)				
Predators	36.48	29.85	39.36	48.61	31.56	53.67	5.24	0.70	0.62	0.01*
	(29.16)	(8.87)	(8.05)	(13.79)	(9.57)	(14.12)				
Philodromidae	2.18	1.17	1.08	9.89	0.70	1.65	1.68	0.54	0.73	0.19
	(0.72)	(0.83)	(0.80)	(9.32)	(0.46)	(0.66)				
Anyphaenidae	0.00	0.51	0.50	0.90	0.39	1.21	0.31	0.35	0.87	0.23
	(0.00)	(0.51)	(0.50)	(0.66)	(0.39)	(1.21)				
Salticidae	2.07	0.68	3.12	0.39	1.75	3.98	0.54	2.82	0.03*	0.31
	(0.94)	(0.44)	(0.74)	(0.39)	(0.24)	(1.12)				

Continued, next page

TABLE 1, Continued

Taxon	Treatment mean (± 1 SE)						MSE	Treatment F	Significance (P)	
	1	2	3	4	5	6			Treatment	Block
Syrphidae	7.78	7.68	1.24	11.17	6.15	2.84	3.94	0.38	0.86	0.01*
	(6.94)	(6.35)	(0.83)	(6.94)	(4.68)	(1.59)				
Bdellidae	6.42	5.93	9.28	3.78	0.69	7.12	1.14	3.11	0.02*	0.39
	(1.35)	(2.45)	(2.97)	(1.18)	(0.47)	(1.77)				
Miridae	1.57	1.29	1.85	0.47	0.87	1.33	0.57	0.22	0.94	0.12
	(1.30)	(0.67)	(1.49)	(0.47)	(0.57)	(0.68)				
Detritivores	144.45	210.34	161.51	128.55	206.18	113.18	19.97	0.59	0.70	0.10
	(31.61)	(67.20)	(28.31)	(18.29)	(58.12)	(23.17)				
Hypogasturidae	14.59	51.29	20.48	19.65	49.32	20.76	22.16	0.14	0.98	0.01*
	(12.27)	(41.68)	(14.77)	(19.21)	(48.73)	(11.05)				
Scapheremaeus sp.	3.50	12.14	4.89	2.82	53.05	6.57	10.34	0.50	0.77	0.01*
	(2.44)	(9.24)	(2.86)	(1.28)	(49.34)	(3.45)				
Sm. *Jugatala* sp.	22.13	12.28	22.40	27.06	34.91	12.11	8.56	0.42	0.82	0.01*
	(9.97)	(5.08)	(12.68)	(14.16)	(17.83)	(4.19)				
Lg. *Jugatala* sp.	43.73	61.29	62.91	30.84	24.70	29.58	13.44	0.67	0.64	0.01*
	(18.07)	(31.76)	(25.71)	(7.44)	(10.23)	(11.13)				
Camisia carrolli	46.26	61.18	36.19	40.86	29.98	24.76	13.85	0.28	0.91	0.01*
	(18.95)	(29.37)	(13.47)	(15.87)	(12.43)	(8.05)				
Psocidae	13.49	10.27	12.94	6.39	12.62	17.09	3.80	0.52	0.75	0.04*
	(6.72)	(3.26)	(5.02)	(3.51)	(2.37)	(8.84)				
Fungivores	0.0	0.31	1.80	1.13	0.0	0.0	0.21	2.39	0.05	0.67
	(0.0)	(0.31)	(1.09)	(0.58)	(0.0)	(0.0)				

the absence of individuals of the species or functional guilds examined. Other block effects were expected and reflect the geographic distributions of these taxa.

Salticid spiders and bdellid mites showed significant pre-treatment differences in abundance. Fewer salticids were found in treatments 2 and 4, and fewer bdellid mites were found in treatment 5 (Table 1). Obviously, when replicate plots are randomly allocated to treatments, random variation should preclude significant pre-treatment differences. Hence, such systematic variation among treatment units prior to the application of treatments suggests type I error. We note that two taxa showing significant pre-treatment differences represent 8% of the taxa analyzed, i.e., nearly the expected type I error rate of 5%. This opportunity to obtain pre-treatment data thus permits adjustment of post-treatment analytical approaches, e.g., analysis of temporal change in abundance among treatments to refine the explanation of treatment effects.

We anticipate that many of the taxa that were sufficiently abundant for pre-treatment analysis will decline in abundance following harvest, as a result of changes in habitat and resource conditions. We also expect many taxa that currently are not sufficiently abundant for analysis to increase in abundance following treatments as habitat and resource conditions become more suitable. Previous studies show that taxa showing significant responses to treatments will represent 30-50% of all taxa (e.g., Schowalter 1994, 1995). Taxa showing non-significant responses to treatment generally have insufficient numbers or have high rates of reproduction and dispersal, leading to relatively even distributions across landscapes.

The results of this study will be used to meet a variety of objectives. Differences in invertebrate abundance between levels of green-tree retention and dispersed and aggregated patterns will provide information on how to better manage our forest ecosystems. Large differences in arthropod abundances due to these treatments will have strong impacts on forest food webs and nutrient turnover. Differences in abundance among the canopy species and functional groups in the overstory and understory will contribute to understanding of the effects of varied levels and patterns of green-tree retention on overall diversity and species representation. Effects on the composition of functional guilds (e.g., defoliator, sap-feeder, fungivore, predator, detritivore) will provide information on potential effects on ecosystem processes. These data, together with information on dispersal capabilities of various taxa, can be used to assess species viabilities, i.e., the ability of dispersed members or subpopulations to attract mates and maintain stable populations. Data on overall above-ground invertebrate diversity will indicate the degree to which varied levels and patterns of green-tree retention can maintain species diversity and particular taxa of concern. Changes in functional guild composition will indicate the degree to which treatments interfere with the spread of potential pests and maintain the abundances of sensitive predator groups, which may contribute to the natural control of potential pests. The impact on detritivores, which contribute to canopy decomposition processes will also be evaluated. Species showing significant changes in density among treatments or through time may be useful indicators of changing environmental conditions.

The data from this study will also contribute to a multi-year data base for canopy arthropod communities in old-growth, partially-harvested old-growth, mature, and regenerating plantations on and near the H. J. Andrews Forest near Blue River, Oregon (Schowalter 1989, 1995) and at the Wind River Canopy Crane site near Carson, Washington. The combined set of data will strengthen our understanding of invertebrate community responses to environmental changes across a 250 km north-south gradient.

Data from this study will be available for integration with other DEMO studies. Measurement of canopy defoliation or estimation of sapsucker abundances and impacts on particular plant species can be related to studies of plant growth and demographics (Halpern et al. 1999). Some plant-associated invertebrates are known vectors of plant pathogens. Measurement of abundance of such groups will be useful in monitoring disease epidemiology. Because many plant-associated invertebrates are major prey items for various vertebrates, especially birds, our data can be used to assess prey availability (Pettersson et al. 1995, Lehmkuhl et al. 1999). Finally, canopy arthropods have important effects on foliage surface area, gas exchange, and microclimate; nutrient cycling and soil fertility; and forest succession (Seastedt and Crossley 1984, Schowalter et al. 1986). These and related data may contribute to development of integrated models for evaluating these ecosystem processes and forest health.

Acknowledgements

We thank Charles Halpern, Richard Goyer, Chris Maguire, Dan Luoma, and two anonymous readers for reviewing this manuscript. We also thank Jim White and Rick Abbott for coordination and assistance in locating the field plots. This is a product of the Demonstration of Ecosystem Management Options (DEMO) study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources.

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Measurement of Differences in Snow Accumulation, Melt, and Micrometeorology Due to Forest Harvesting

Abstract

Previous studies in the Pacific Northwest have suggested a link between forest logging and increased streamflows. We present a brief overview of previous experimental efforts designed to identify mechanisms for these increases, especially during rain-on-snow (ROS) and spring snowmelt events. To extend the applicability of these data, we describe our measurement of snow accumulation, melt, and micrometeorology in existing uncut forest and shelterwood units as part of the Demonstration of Ecosystem Management Options (DEMO) study. Uncut forest units are dominated by over 100-year-old Douglas-fir (*Pseudotsuga menziesii*) with stand basal areas of ca. 40 m^2/ha. Micrometeorology is measured 2 m above the ground surface in each 13-ha unit. Snow accumulation and melt are measured via weekly snow courses. Snowpack outflow is obtained from two 2.6 m^2 non-weighing snow lysimeters in each unit. Large (25 m^2) weighing lysimeters provide a continuous record of snowpack evolution at scales unaffected by variability in canopy throughfall. Snow interception is measured by continuous weighing of cut trees. Harvest treatments will be imposed during summer 1998 and additional post-harvest data will be collected. Pre-harvest data indicate up to 60% greater (33 mm) 3-day production of runoff and 150% greater (22 mm) 3-day snowmelt (outflow minus throughfall) in the shelterwood than in the uncut forest unit during ROS events. Snowmelt during radiation-dominated spring events is ca. 50% greater (15 mm) in the shelterwood. Results from the weighing lysimeters show high correlation with snow course data from the shelterwood but poor correlation with those from the uncut forest due to small scale spatial variability in tree canopy cover.

Introduction

In recent years, attention to floods during rain-on-snow events has increased. During the winters of 1986, 1990, and 1995-97, the major rivers draining the western Cascade Mountains of Washington and Oregon experienced flooding events with estimated return periods that exceeded 100 years in some watersheds. These events have lead to a widespread perception that the frequency and severity of extreme floods in the Pacific Northwest have increased. Although these perceived increases may be due to climate variability, which has brought an end to the mild, relatively dry winters of the 1970s and 1980s, attention has nevertheless been focused on possible causal links with land use changes, including forest harvesting. Although the connection between forest harvest and increased peak streamflow has only recently gained the attention of the media and the general public, the problem has long been debated in the scientific literature (e.g., Anderson and Hobba 1959; Rothacher 1973; Harr and McCorison 1979; Harr 1981, 1986; Christner and Harr 1982; Jones and Grant 1996).

Anderson and Hobba (1959) appear to be the first to argue that the size of peak flows in western Oregon had been increased by logging. Despite considerable research on snow hydrology in the intermountain west and the Sierra Nevada (where snowmelt is dominated by radiation), the issue of logging effects on snow hydrology in the Pacific Northwest was largely ignored until the 1980s. Building on the work of the USACE (1956), Harr (1981) hypothesized that clearcut logging would increase convective heat transfer to the snowpack and thereby enhance snowmelt rates, especially during rain-on-snow (ROS) events. Through a reanalysis of previous work (Rothacher 1973, Harr and McCorison 1979) in which no effects were detected, Harr (1986) found that peaks in streamflow during ROS events increased significantly due to clearcutting. Christner and Harr (1982) also found evidence for an increase in ROS-induced peak streamflows in an analysis of paired watersheds in the central Oregon Cascades (see also Jones and Grant 1996). Although these studies offer considerable evidence for the effects of forest harvesting on streamflows within a small watershed, they only suggest possible mechanisms for the increase.

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Subsequently, in the transient snow zone of the western Oregon Cascades, a series of plot-scale studies (i.e., at the scale of several trees) demonstrated that snow accumulation can be significantly enhanced in clearcut areas (Berris 1984, Berris and Harr 1987). However, in three of five ROS events more snowpack outflow was observed under the forest canopy than in the clearcut. In the remaining two events, the increase in clearcut snowmelt can arguably be attributed to more antecedent snow in the clearcut and not to higher melt rates during the event. Unfortunately, the relatively small area of the snow lysimeters (2.0 m^2) precluded accurate estimation of snowpack outflow underneath the forest canopy for any of the events.

Equivocal results were also obtained from studies in the coastal mountains of British Columbia (Beaudry and Golding 1983). Outflow from two small snowmelt lysimeters with a combined area of 0.9 m^2 had almost no correlation with weekly snow course data. In contrast, large lysimeters (28 m^2) indicated that total runoff from the clearcut snowpack was increased by 10% during heavy rain (194 mm rainfall in 1.5 days) and by up to 19% for smaller events. In two of three events, differences in outflow can be attributed to both differences in melt rates and antecedent snow accumulation.

Recognizing the limitation in design and the small sample size of previous studies, a second more extensive plot-scale study was undertaken in the transient snow zone of northwestern Washington (Coffin and Harr 1992). Unfortunately, a series of logistical and design problems combined with unseasonably cold weather made comparisons among treatments (clearcut versus uncut forest) questionable for the majority of observed ROS events. During four ROS events in which the sample size under the mature canopy was sufficient, 12-44% greater runoff in the clearcut was arguably due to both increased melt rates and greater antecedent snow accumulation.

Combined, these studies present considerable evidence that removal of the forest canopy increases snow accumulation and melt by influencing the moisture and energy fluxes from the forest canopy to the forest floor. Snow is intercepted by the forest canopy and can be subsequently sublimated, melted or released (as snow) off the canopy (e.g., Miller 1962, Satterlund and Haupt 1970). While sublimation represents a direct loss from the soil-snow system, drip of melt-water from the canopy is either stored by the snowpack or routed directly to the soil (depending on the snowpack temperature and liquid water content). Snow released from the canopy adds directly to the water equivalent of the snowpack.

Melt of the ground snowpack is affected by removal of the canopy through the following mechanisms. The canopy greatly attenuates short-wave radiation to the ground surface while enhancing long-wave radiation transfer (e.g., Black et al. 1991). Short-wave radiation absorbed by the canopy is re-radiated to the snowpack as long-wave radiation. Furthermore, the canopy serves to shelter the snowpack from turbulent exchanges of latent and sensible heat which depend directly on windspeed and the near surface gradients of temperature and humidity. During events in which short-wave radiation and turbulent energy fluxes prevail, canopy removal enhances snowmelt. However, the canopy can also hasten snowpack outflow. Because intercepted snow melts rapidly in the transient snow zone, snowpacks under a forest canopy tend to be shallower with higher liquid water contents. Therefore, they can release meltwater or rainfall sooner than snowpacks in clearings (e.g., Berris and Harr 1987)

Given the complex interaction of the forest canopy with meteorological conditions and the transient nature of snow accumulation on and under the forest canopy, previous studies have provided only limited information relevant to a quantitative model of snow accumulation and melt under forest canopies (e.g., van Heeswijk et al. 1996). Snowpack outflow during melt events is influenced by antecedent snow accumulation on the ground, antecedent snow storage in the forest canopy, and the micrometeorological conditions. Therefore, additional studies are needed to more completely characterize the full range of expected differences between harvested and uncut forest sites.

Previous studies that compare clearcut and uncut forests are also of limited value in that current harvest practices have become more diverse and now include a range of levels and patterns of retention of live trees (i.e., green-tree retention). Thus, the effect of canopy density on snow accumulation and melt has become an important question. Currently, variation in forest canopy cover

is largely ignored in determining the hydrological effects of logging. For example, the Washington State watershed analysis procedure (WFPB 1994) utilizes an overly simple model for predicting snowmelt during ROS events which assumes that wind speed is a linear function of canopy coverage. Because canopy coverage is based solely on stand maturity, hydrologic impacts of partial harvests are not considered. This limitation is not surprising considering the lack of data relating partial harvest to expected snowmelt production in the Pacific Northwest.

Recently, more advanced, quantitative models have used an energy-balance approach to predict snowmelt given a set of micrometeorological variables and antecedent snowpack conditions (Anderson 1976, Marks and Dozier 1992, Yamazaki and Kondo 1992, Wigmosta et al. 1994). However, under-canopy snowmelt and micrometeorological data of sufficient high quality necessary for model validation have been unavailable in the Pacific Northwest (van Heeswijk et al. 1996). A further limitation of these models is that they largely ignore the effect of the canopy on snow accumulation. Unless antecedent conditions can be described, their value as a predictive tool is limited.

Objectives

To address the limitations and expand the applicability of previous data, we have been evaluating changes in snow accumulation and snowmelt in response to partial retention harvests within the context of the Demonstration of Ecosystem Management Options (DEMO) study (Aubry et al. 1999). To review, at each of eight study blocks in western Washington and Oregon, five harvest treatments and a control have been randomly assigned to 13-ha experimental units. Treatments represent retention of green trees at varying levels (15-100% of original basal area) and patterns (trees uniformly dispersed vs. aggregated in 1-ha patches) (Aubry et al. 1999). The specific objectives of the snow hydrology studies are to:

(1) Determine the differences in accumulation of snow under varying levels and patterns of green-tree retention,

(2) Identify differences in outflow rates among treatments during rain-on-snow events,

(3) Identify differences in melt rates during spring radiation-dominated events,

(4) Measure the differences in wind, temperature, humidity, radiation, and turbulent heat exchange among treatments, and

(5) Provide data to improve existing models of snow accumulation and snowmelt at both point (single tree) and stand-level (13-ha treatments) scales of resolution.

Each season of data collection strives to provide a continuous record of near-surface micrometeorology and snowpack outflow at several points in each unit while providing weekly data on snow accumulation over the entire unit. Objective 1 relies on snow course data taken over the 13-ha treatment unit. Point observations of micrometeorology and snowpack outflow support Objectives 2-4. Objective 5 can be satisfied by calibrating a snow accumulation and snowmelt model to point measurements and validating against data over the entire unit. The degree to which alteration of physically measurable parameters such as canopy coverage fraction can explain differences between point observations of melt and areal observations of accumulation will directly test the scalability of such a model.

Micrometeorological and snow data have been collected in uncut, pre-treatment forests and in adjacent shelterwood stands (forest thinned to very wide spacings) at one of the eight experimental blocks, Watson Falls, Oregon. Due to the large number of treatments, the sample size and frequency of the current experimental design are limited. The expense of collecting detailed meteorological and outflow data limits us to one micrometeorology station and four lysimeters per treatment unit. Snow course data are collected weekly. Harvest treatments will be completed during summer 1998 and each harvest unit will then be instrumented with four lysimeters and one micrometeorological station. Three years of post-harvest data will be collected to quantify the effects of varying levels and patterns of canopy retention.

Given the limitation on sampling within each unit and the lack of treatment replication, we may be unable to make definitive statements about the significance of specific treatments on snow accumulation and snowmelt. Although we can detect differences in outflow from an uncut mature forest and a shelterwood (see Results and Discussion), more subtle differences (as would be expected between a 40 and 75% retention harvest) may be undetectable (or insignificant) given

our small sample size. Furthermore, the lack of treatment replication (in the snow hydrology study) limits the applicability of findings to the specific units studied. Although the treatment units were selected to be as similar as possible, the lack of replication makes it impossible to differentiate treatment effects from other site level differences (e.g., aspect, exposure to prevailing winds). A true test of treatment effects will require data from replicated samples.

In the following sections we briefly describe the study sites and detail the data collection method. We then present a brief comparison of data from the pre-harvest DEMO units and adjacent shelterwoods. Finally, we describe additional data collection efforts aimed at quantifying process-level controls on snow accumulation and melt (e.g., canopy interception) and the preliminary results of this work.

Methods

Site Description

The study sites are located northwest of Crater Lake, Oregon in the Umpqua National Forest (Figure 1) (see also Aubry et al. 1999). Three DEMO treatment units (2, 5, and 6) are located at 900 m elevation and two (1 and 4) at 1200 m. An additional control treatment (7) is sampled at the low elevation site. Unit 3 (not shown in Figure 1) is not utilized due to difficulties with winter access. To provide a more extensive period during which snow accumulation and melt could be compared between uncut and harvested sites, an additional shelterwood was selected in each elevation band (units 8 and 9).

Pretreatment forest stands range in age form 110-130 years. The canopy is dominated by Douglas-fir (*Pseudotsuga menziesii*) although

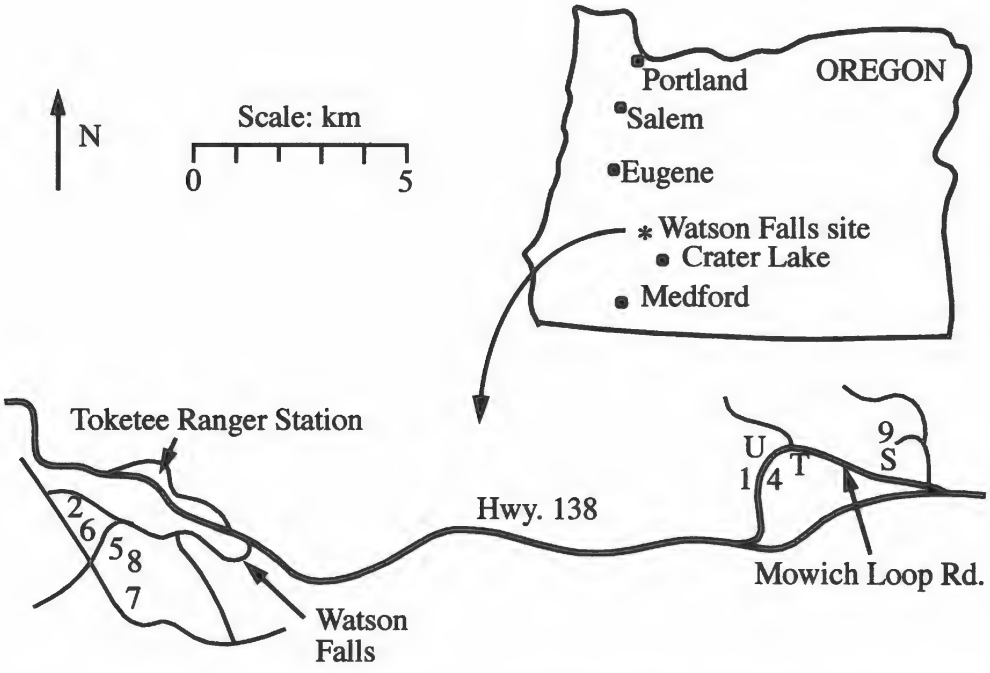

Figure 1. Locations of DEMO green-tree retention units (1, 2, 4-6), other non-experimental units (7-9), and weighing lysimeters (U, S, T) at the Watson Falls study site. U = intact forest, S = shelterwood, and T = tree-weighing lysimeter. Treatment 3 is not utilized for snow hydrology research.

white fir (*Abies concolor*), western hemlock (*Tsuga heterophylla*), and ponderosa pine (*Pinus ponderosa*) are fairly common. Basal areas in the DEMO treatment units range from 36 - 52 m^2/ha (see Halpern et al. 1999 for details).

Micrometeorology

The measurement of forest micrometeorology during winter presents unique difficulties (e.g., Marks et al. 1992). Our sampling and instrumental designs are similar to those of Berris and Harr (1987) and Coffin and Harr (1992). Micrometeorology is measured 2 m above the soil surface and summary statistics are recorded every 30 minutes. Precipitation is measured with a resolution of one millimeter by an unheated gauge. The gauge consists of a 30.5 cm diameter length of PVC pipe 1.2 m tall attached to a rigid PVC base. The gauge is filled to a depth of 25 cm with an antifreeze solution that is a 3:2 mixture of propylene glycol and ethanol (McGurk 1992) topped with a thin layer of 10-30 weight motor oil to prevent ethanol evaporation. The antifreeze is recharged after 500 mm of precipitation to limit dilution and thereby prevent freezing. Outflow from the reservoir is collected by a tipping bucket. To limit catch deficiencies, each gauge is shielded from the wind.

Wind speed is measured with R.M. Young photochopper totalizing anemometers. These measure wind passage each minute and therefore effectively integrate the wind velocity over the observational interval. To prevent snow accumulation on the anemometers, housings were constructed consisting of a 30 by 30 cm square of Plexiglas suspended approximately 15 cm above the anemometer. Comparison of paired anemometers with and without housings showed no noticeable difference in wind speed when the unprotected anemometer was free of snow.

Incoming short-wave radiation is measured with Epply pyranometers. Reflected short-wave radiation, measured with Licor silicon cell pyranometers, is used to estimate albedo and to correct the Epply pyranometers when they are covered with snow. Incoming long-wave radiation is measured by Epply pyrgeometers. Air temperature and relative humidity are measured by Campbell Scientific Vaisala probes protected from direct and reflected radiation by six plate shields.

Snowmelt

Snowpack outflow is measured every 30 min by a non-weighing snow lysimeter with a surface area of 2.6 m^2 which is drained to a 1-l capacity tipping bucket. The lysimeter is lined with an impermeable geo-textile lining (hypalon). A plastic drain is installed flush with the liner in one corner of the lysimeter. The drains, piping, and tipping buckets are buried to prevent freezing. Shadecloth is draped over each lysimeter to prevent litter accumulation from clogging the drains.

Snowmelt is estimated as the difference between snowpack outflow and precipitation. Unfortunately, this calculation is only valid if two assumptions are met. First, any rain falling on the snowpack, along with any melt water, is immediately routed out of the snowpack. Second, precipitation rates over each lysimeter under the canopy are well approximated by estimates of canopy throughfall or precipitation in the open. The first assumption is generally met if snowpacks are shallow, isothermal at 0°C, and at their maximum liquid water holding capacities. Snowpacks in the transient snow zone of the Cascades generally meet these assumptions. If they do not, however, melt rates will be underestimated. Unfortunately, the second assumption is less likely to be valid. Given the high spatial variability of throughfall from a forest canopy, point estimates of precipitation are subject to significant error. Therefore, only measured precipitation from the shelterwood sites is used to estimate snowmelt. Although observations of lysimeter outflow under the canopy are subject to this same variability, they are more robust due to their larger surface areas.

Snow-water Equivalent

Direct observations of snow depth and snow-water equivalent (SWE) are taken in each treatment unit. During winter 1993-94, snow depth was measured at 25 points (80 by 80 m spacing) in each of the five low elevation units at the Watson Falls study site. These data were used to determine the number of sample points needed to detect a 5 cm difference in snow depth (not water equivalent) with a power of 0.7 at $P \leq 0.05$. A minimum of 17 sample points per unit are adequate, thus snow courses are run over a 20-point grid. Water equivalence is obtained with a standard U.S. snow tube. Snow course measurement

and sampling procedures follow Natural Resource Conservation Service guidelines (USDA-SCS 1984).

Canopy Processes

Due to the coarse temporal resolution of the snow courses and the small surface areas of the lysimeters in each treatment, our sampling design is insufficient for rigorous testing of models of snow accumulation and ablation. Although many small lysimeters can characterize the average outflow of a harvest unit and its variability, they cannot fully describe processes at the scale of an individual tree canopy. Since canopy throughfall is highly variable at small spatial scales, any estimate of snowmelt (outflow minus throughfall) measured by small lysimeters may not be representative of the canopy as a whole. Furthermore, because snow accumulation is affected by snowfall, melt, and mass release from the canopy, weekly snow course measurements yield little information on snow interception processes that control snow accumulation. While a model of under-canopy snow accumulation and melt can be used to test the combination of all three factors, the current design (and those used by previous investigators in the Pacific Northwest) does not allow for the separation of effects. Such separation would require continuous measurement of snowpack outflow and water equivalent at a scale at which variability in canopy throughfall no longer dominates observations.

To overcome these limitations, we began a pilot study during winter 1996-97 to extend the existing field program. Two 25 m^2 weighing lysimeters were constructed. Each lysimeter was installed around a ca. 40-m-tall Douglas-fir adjacent to Unit 1 (Figure 2). The lysimeter is continuously weighed by four, 5-ton load cells. Outflow from the lysimeter is measured with tipping-bucket volumetric flow gauges. The weighing lysimeter effectively removes the variability in throughfall by sampling the entire canopy of at least one mature tree while directly measuring changes in

Figure 2. Overview of the under-canopy weighing lysimeters showing 25 m^2 lysimeter, micrometeorological station, and precipitation gauge.

the snowpack water equivalent. Two weighing lysimeters were built to control for inter-canopy variability and equipment failure.

While the weighing lysimeters can generate high-quality data on snow accumulation and ablation under the forest canopy, they cannot, by themselves, provide information on the processes controlling snow interception, mass release, or drip of meltwater to the ground snowpack. To more completely investigate snow interception, one smaller (12.5 m^2) weighing lysimeter was placed in the open, in the upper elevational shelterwood unit. Snow interception and release is then inferred by comparing the SWE of the two weighing lysimeters under the tree canopy to that of the shelterwood lysimeter. To measure snow interception directly, we installed two "cut-tree" experiments similar to those described by Schmidt (1991) and Lundberg (1993) in a forest plantation adjacent to the DEMO units (Figure 1).

Results and Discussion

Pre-treatment Snow Course Data

Weekly snow courses taken during the pre-harvest data collection period can be used to assess treatment level variation, as well as differences between uncut and shelterwood stands. Comparison of data from the high-elevation shelterwood and two nearby uncut units shows that gross accumulation and rate of melt tend to be greater in the shelterwoods (Figure 3a). Inter-annual variability was high, reflecting the timing and magnitude of winter storms. During 1995-96, significant snowfall and accumulation did not occur until January during a series of intense storms. These large events overwhelmed canopy interception and deposited nearly equal amounts of snow in both open and forested areas. In contrast, during winter 1996-97, snow accumulation occurred during many smaller storms. During these small events the forest canopy intercepted a significant fraction of total snowfall. These differences in interception efficiency with storm size have been previously observed (e.g., Satterlund and Haupt 1967, Schmidt and Gluns 1991). Interception efficiency increases initially with snowfall as needles and branch tips are bridged by snow, thereby increasing the interception surface area. However, as snowfall continues, interception efficiency decreases as snow loading overcomes branch stiffness and adhesive-cohesive bonds.

Although interception efficiency controls the retention of snow by the canopy, subsequent melt of intercepted snow controls snow accumulation under the forest canopy. This is evident in the reduced SWE beneath the uncut forest canopy relative to that of the shelterwood unit (Figure 3a). Although sublimation rates of intercepted snow can approach several mm per day in cold climates (Schmidt 1991, Lundberg 1993), opportunities for sublimation of intercepted snow are limited in the transient snow zone of the Cascades. Observations during frequent field visits suggested that melt of intercepted snow and subsequent drip to the ground snowpack were rapid (typically achieving complete removal within 24 hr).

Our observation that a sparser canopy results in reduced SWE is supported by a comparison of snow course data from the two uncut forest sites (Units 1 and 4) at 1200 m (Figure 3b). Although these sites are adjacent and were selected to be as similar as possible, they differ in forest structure. The trees in Unit 4 are larger on average than those in Unit 1 (C. B. Halpern, pers. comm.) and they support fewer branches at lower positions on the trunk (pers. obs.). During winter 1995-96, when early-season differences in snow accumulation between the shelterwood and the two uncut forest sites were minimal, the latter two also behaved almost identically until the melt event in early February. After this event, melt was more rapid under the taller, sparser canopy of Unit 4 (Figure 3b). A similar trend was observed during the following year. The variability of snow course data from two ostensibly similar forest stands underscores the necessity of collecting several seasons of pre-harvest data before inferences can be drawn on the effects of forest harvesting.

Meteorological and Lysimeter Data

Although the weekly snow course measurements provide a reliable estimate of accumulation at the scale of the treatment unit (13 ha), they provide little direct evidence for significant increases in water delivery to the soil during the relatively short periods (one to three days) of ROS or radiation-dominated melt events. This information is available from the snow lysimeters and micrometeorological stations. Unfortunately, since continuous measurement of snowpack within a 13-ha treatment unit is not feasible, the lysimeter data are by necessity limited to point estimates. Moreover,

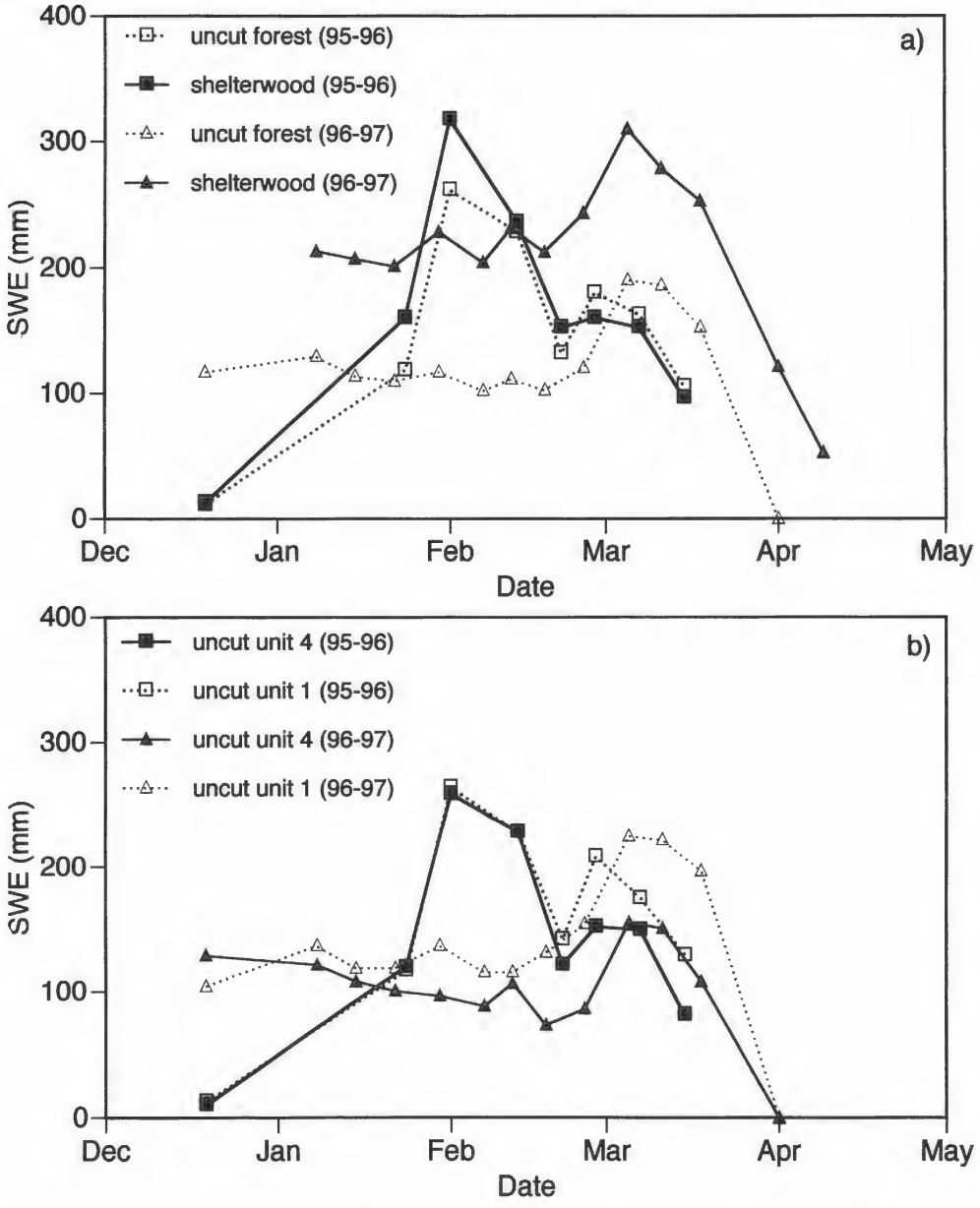

Figure 3. a) Snow course data during winter 1995-96 and 1996-97 for a shelterwood stand (Unit 9) and two uncut forests (average of Units 1 and 4). b) Variability in snow course data in the two uncut forest units (1 and 4) during winter 1995-96 and 1996-97.

because of their relatively small surface area (2.6 m^2), estimates from individual lysimeters are strongly influenced by their position under the canopy. This variability can be estimated by examining large numbers of lysimeters. For the results described below, outflow from the shelterwood represents the average of two adjacent lysimeters (neither is directly beneath a tree canopy); outflow for the uncut forests represents the average of four lysimeters at 1200 m or five lysimeters at 900 m. Comparisons of outflow, precipitation, and micrometeorology are limited to units of similar elevation.

Rain-on-snow Event

A ROS event occurred at the upper units (1, 4 and 9) during February 1996 (Figure 4a). During the event, average precipitation in the shelterwood and forested units was nearly identical (32 and 36 mm, respectively). However, snowpack outflow was greater at the shelterwood site than the uncut forest (89 and 56 mm, respectively). This corresponds to 59% greater snowpack outflow and 150% greater snowmelt due to shelterwood harvest. Near-surface micrometeorological data show noticeable differences between the shelterwood and uncut units (Figure 4b, c). Near-surface wind speed and air temperature were greater in the shelterwood than the uncut forest leading to increased melt rates in the former. Incoming long-wave radiation was nearly identical for both sites. Short-wave radiation was greater in the shelterwood than beneath the uncut forest and contributed to increased melt rates during the afternoon of 7 February.

A larger ROS event occurred over six days in late December 1996 and early January 1997 (Figure 5). The average precipitation recorded in the shelterwood was 165 mm. Average accumulated snowpack outflow was greater in the shelterwood (312 mm) than beneath the uncut forest (250 mm) (Figure 5a). This corresponds to 25% greater snowpack outflow and 72% greater snowmelt due to shelterwood harvest. Once again, near-surface meteorology shows considerable differences between the shelterwood and uncut forest sites (Figure 5b, c). Incoming long-wave radiation was greater beneath the uncut forest, especially during evening hours. Air temperature and windspeed were greater in the shelterwood than beneath the intact canopy, most noticeably during periods corresponding to maximum differences in snowpack outflow.

Individual lysimeter outflows during ROS events were highly variable. For example, during the period from 6 to 9 February 1996 (Figure 4a) the two shelterwood lysimeters at 1200 m recorded total outflows of 102 and 88 mm. Under the uncut forest canopy, variability was noticeably greater. Lysimeters in Unit 1 recorded outflows of 51 and 42 mm and those in Unit 4, 76 and 75 mm. Greater outflow under the sparser canopy of Unit 4 is consistent with the more rapid melt observed in the snow course data. Similar variability was observed at the lower elevation site during the same event. The shelterwood yielded outflows of 121 and 135 mm while the uncut forest yielded outflows of 72-99 mm. A non-parametric rank sum test to test the null hypothesis that outflow rates are similar in the shelterwood and uncut forest (at 1200 m) indicates that outflow in the shelterwood is greater than under the uncut forest ($p<0.1$).

Radiation-dominated Event

During a radiation-dominated snowmelt event at the high elevation site, three-day snowmelt volumes were 44% greater in the shelterwood site than beneath the uncut forest (Figure 6a). This increase corresponded to the greater net (incoming minus outgoing) short-wave radiation in the shelterwood than beneath the uncut forest (Figure 6b). However, net long-wave radiation was consistently greater beneath the uncut forest than in the shelterwood. In fact, beneath the intact canopy, net long-wave radiation represents a larger energy flux than net short-wave radiation over the entire event. The full canopy absorbs incoming short-wave radiation during daylight hours and radiates this energy as long-wave radiation during the evening. Consequently, during the evening of 7 March and the morning of 8 March, snowmelt rates at the uncut forest unit were greater than in the shelterwood unit. Since the net long-wave flux at the uncut site was near zero, even small fluxes of sensible or latent heat to the snow surface were translated directly to melt. (Although not shown in Figure 6b, air temperatures remained above freezing with light winds throughout the evening.) At the shelterwood site, the negative (i.e. away from the snow surface) flux of long-wave radiation prohibited melt.

Weighing Lysimeters

The results of our pilot study to measure canopy processes at the scale of an individual tree illustrate

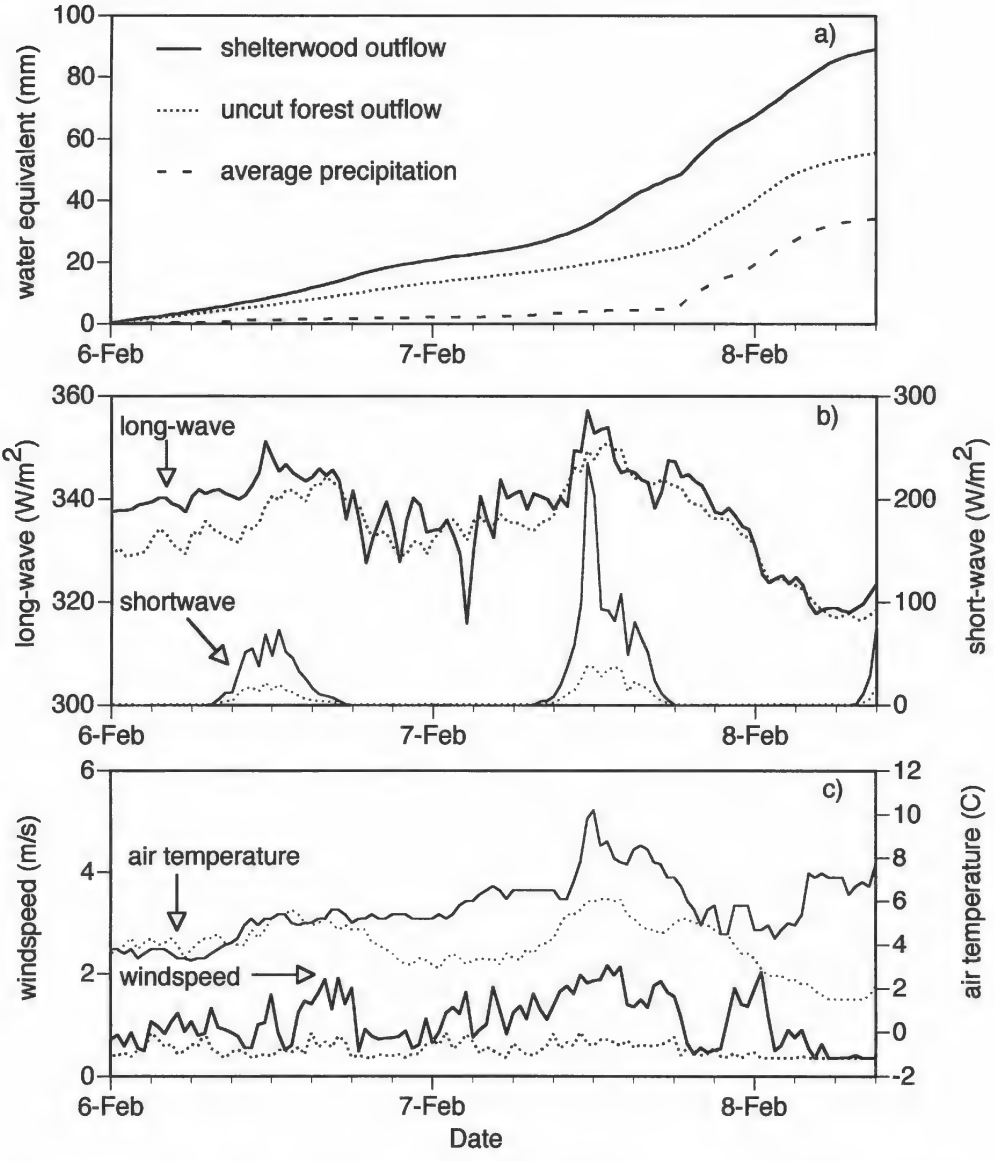

Figure 4. a) Accumulated snowpack outflow for uncut forests (average of Units 1 and 4) and a shelterwood site (Unit 9), and precipitation (Unit 9) during a rain-on-snow event, February 1996. b) Incoming short- and long-wave radiation for the same sites and period (solid lines are shelterwood, dotted lines are uncut forest). c) Air temperature and windspeed for the same sites and period (solid lines are shelterwood, dotted lines are uncut forest).

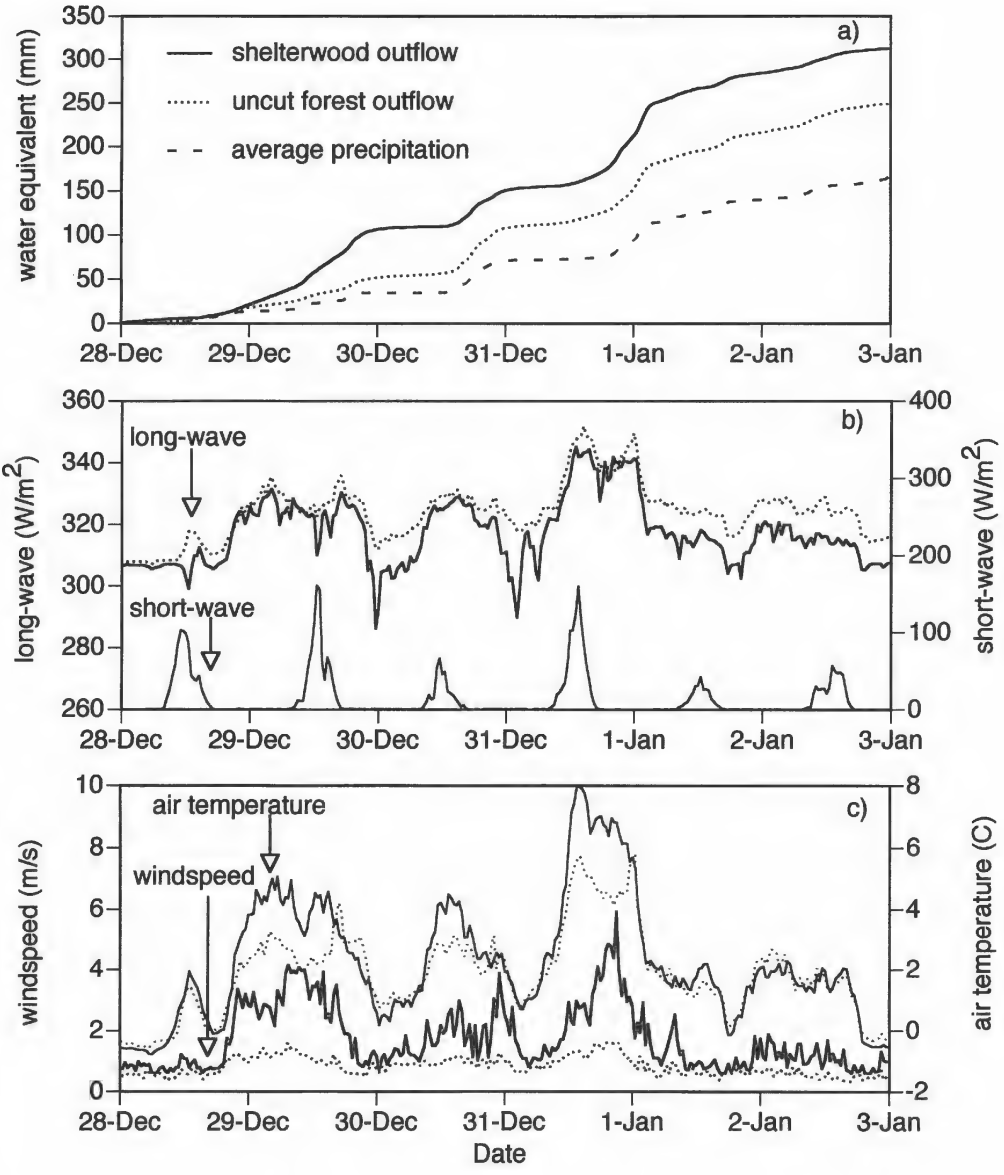

Figure 5. a) Accumulated snowpack outflow for uncut forests (average of Units 1 and 4) and a shelterwood site (Unit 9), and precipitation (Unit 9) during a rain-on-snow event, 1996-97. b) Incoming short- and long-wave radiation for the same sites and period (solid lines are shelterwood, dotted line is uncut forest). c) Air temperature and windspeed for the same sites and period (solid lines are shelterwood, dotted lines are uncut forest).

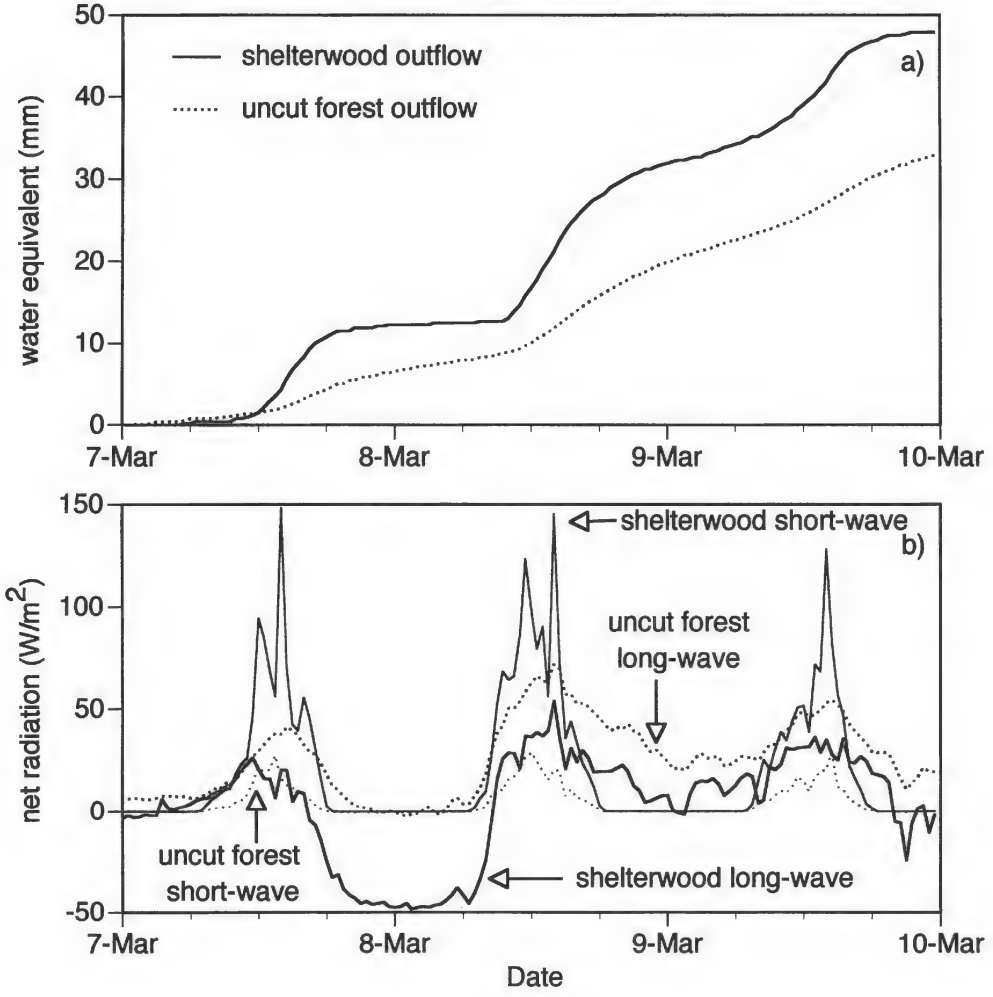

Figure 6. a) Accumulated snowmelt for uncut forests (average of Units 1 and 4) and a shelterwood site (Unit 9) during a spring snowmelt event, March 1996 (solid line is shelterwood, dotted line is uncut forest). b) Incoming net short- and long-wave radiation for the same sites and period. Net short-wave radiation is based on measured incoming and an observed albedo of 0.75. Net long-wave radiation is based on measured incoming and assumes that the snowpack acts as a blackbody emitter at 0°C (solid lines are shelterwood, dotted lines are uncut forest).

that the weighing lysimeters are capable of continuous measurement of SWE and snowpack outflow (Figure 7). The overall effect of the canopy on seasonal snow accumulation was dramatic. During the early accumulation season, canopy interception and subsequent melt limited the under-canopy SWE to approximately 50% of the shelterwood value. Loss of SWE during the ROS event of 1 January 1997 is clearly shown. Canopy interception and snowmelt were even more dramatic during the secondary snow accumulation period (beginning on 1 February). During this

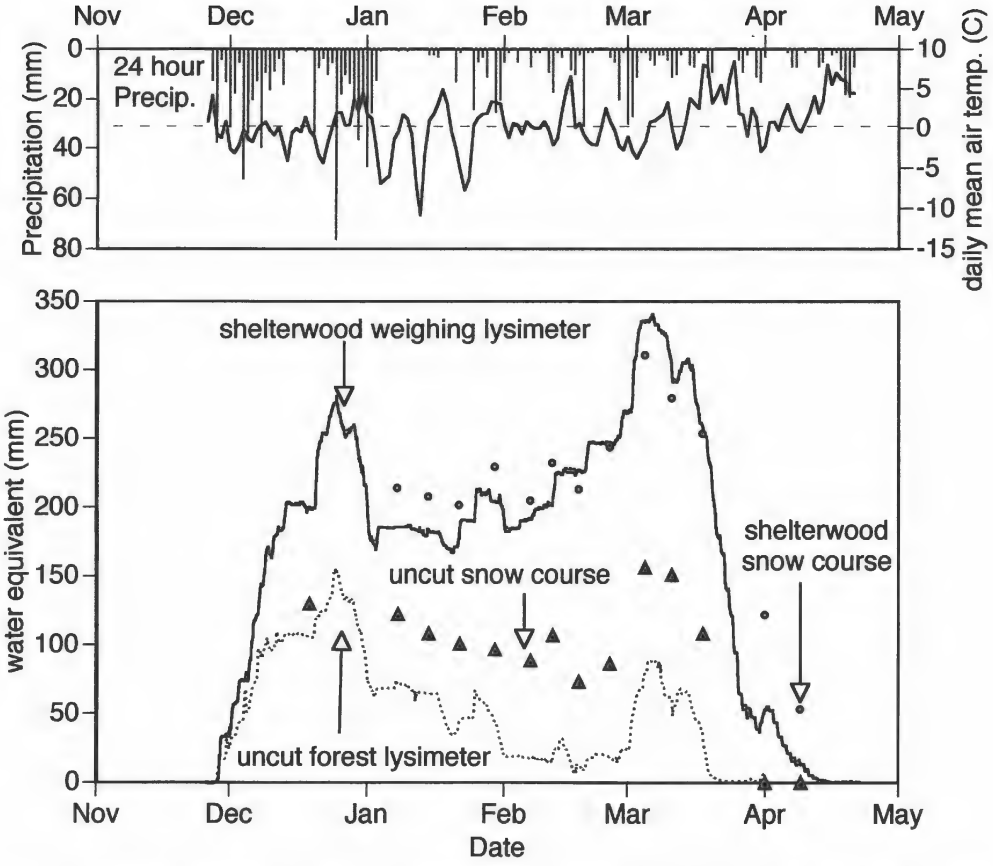

Figure 7. Precipitation, temperature, and weighing lysimeter data for shelterwood and uncut forest sites during 1996-97. Snow course data from shelterwood (Unit 9) and uncut forests (average of Units 1 and 4) during 1996-97.

period, the majority of snowfall occurred near freezing. While significant snow accumulated at the shelterwood site, there was no snow accumulation under the canopy until the snowfall of 1 March, which occurred at much colder temperatures.

Snow course data correlate well with the continuous measurement of SWE in the shelterwood site but poorly under the intact canopy. The relatively poor agreement of the latter is best explained by the dependence of snow accumulation on canopy coverage. Although each canopy lysimeter was situated entirely under a continuous canopy, the average unit canopy closure was ca. 80%. Thus, as the snow course samples the entire treatment unit and the weighing lysimeters sample under a full canopy, we would expect the observations of snow accumulation to differ. However, this difference provides a unique opportunity for model validation. Any model of snow accumulation and melt under a forest canopy should account for this difference through its parameterization of canopy closure. Given the success of the pilot program in continuously measuring SWE during the accumulation and melt season, we are continuing the weighing lysimeter experiment to supplement the data collected by the snow courses and non-weighing lysimeters.

Acknowledgements

The first author has received support from a NASA Earth System Science Fellowship. Many individuals

have contributed to various aspects of this research. We would especially like to thank those who have collected snow course data: Joe Brett, Beth Evans and John Scott. Rick Abbott has been especially helpful in facilitating field work and site access. Critical reviews of this paper were provided by Matt Brunengo, David Post, Jim White, and three anonymous reviewers. This is a product of the Demonstration of Ecosystem Management Options (DEMO) study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources.

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Regeneration Harvests Versus Clearcuts: Public Views of the Acceptability and Aesthetics of Northwest Forest Plan Harvests

Abstract

The Northwest Forest Plan, "New Forestry," and the "regeneration harvests" they prescribe offer some potential resolution to long-standing adverse perceptions of clearcut logging. This study investigated prospects for this potential resolution preliminary to more robust findings from a larger social perceptions study in progress. Ratings of acceptability and scenic beauty for depictions of timber harvests with aggregated and dispersed patterns of about 15 percent green-tree retention were acquired from a diverse sample of adults in western Oregon and Washington. Respondents rated actual photographs and simulated scenes showing the two retention patterns as well as clearcuts and uncut forests shown in the same scenes. Respondents rated the green-tree retention scenes with and without information about their "New Forestry" attributes and intentions. Comparisons of the average ratings suggest that 15 percent green-tree retention harvests can be perceived much the same as clearcuts. Public education is needed to improve perceptions of the acceptability of retention harvests. Aggregated green-tree retention patterns within harvests may help to produce more favorable perceptions of scenic beauty.

Introduction

The management of national forests in the Pacific Northwest is becoming more complex and political. The spotted owl controversy (Dietrich 1992) and its current resolution in the Northwest Forest Plan (USDA and USDI 1994) has shifted the technical emphasis of forest planning away from traditional silvicultural goals toward large-scale biodiversity goals. The complex decisions that arise from these often conflicting goals are now mediated through notions of "ecosystem management" (Bengston 1994, Vogt et al. 1997) and "New Forestry" (Gillis 1990, Kohm and Franklin 1997), in response to public demands for more multiple-value, sustainable resource management (Steel et al. 1994, Jones et al. 1995, Durbin 1996). The intensity of conflicts over forest management and of the politics that generated the Northwest Forest Plan indicate that the social acceptability of its prescriptions will likely play a key role in its implementation (Stankey and Clark 1992).

The social acceptability of forest management is complex (Brunson 1993, Gobster 1995). One critical dimension involves how recent timber harvests are visually perceived (Ribe 1989, Gobster 1994). Visual perceptions of acceptability often tend to derive from aesthetic reactions (Nassauer 1992). These perceptions are generally understood to be a primary cause of public reactions to forest management (Ulrich 1986). Aesthetic perceptions affect acceptability perceptions among more disinterested observers who are thereby disposed mainly to aesthetic responses (Santayana 1896, Zajonc 1980), such as recreational visitors or passers through lacking a strong or active proprietary or ideological interest in national forests (Ulrich 1983). Or, public perceptions of management may be more cognitive, involving conceptual understandings or associations with what is seen, such as ecological impacts, the perceived virtue of forestry practices, or other normative ideas (Brunson 1993, Gobster 1996). These cognitive perceptions are based upon what philosophers and psychologists identify as more interested, as opposed to disinterested, observation which is less conducive of strongly or purely aesthetic responses (Santayana 1896, Izard 1977). Aesthetics is a recurring issue in forest policy (Dana and Fairfax 1980, Wilkenson and Anderson 1987). Much political opposition to national forest management has centered on perceptions of clearcut logging (Hays 1987, Hirt 1994). Photographs of clearcuts have appeared in countless popular media and political advocacy publications affecting national forest policy. Some examples are the Oregonian newspaper (1990), Devall (1994) and Native Forest Council (1987-98). Clearcuts are offered as evidence of excessive resource exploitation or destruction of functioning ecosystems (Wood 1971, Fritz 1989).

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New Forestry offers alternatives to clearcuts, and the Northwest Forest Plan (NFP) prescribes one such alternative. It prescribes that living trees be retained within 15 percent of the area within each harvest unit, at least 70 percent of this retention be left in clumps, and that down wood be retained according to forest types (USDA and USDI 1994, p. C-39-41). These "regeneration harvests" seek to retain "biological legacies" (live and dead vegetative structures) to aid recovery and stability of biodiversity and ecosystem function following harvests (Perry and Amaranthus 1997). They will likely be the most visually noticeable manifestation of the NFP in the landscape, and a centerpiece for public perception of the acceptability of Forest Service management guided by that plan. The prospective nature of those perceptions is the focus of the social perceptions component of the Demonstration of Ecosystem Management Options (DEMO) study. DEMO is a replicated, long-term experiment that investigates many ecological and social consequences of several amounts and patterns of green-tree retention during harvests in western Washington and Oregon.

A Prospective Study

The social perceptions component of the DEMO study is yet to be completed. It will investigate perceptions of photographs of pre-harvest forests and of the different magnitudes and distributions of green-tree retention in the DEMO experimental harvests. Photographs of clearcuts with various volumes of woody debris retention from the Long Term Ecosystem Productivity (LTEP) study and various thinnings from the Young Stands Study (YSS) will also be included in this upcoming study. Perceptions of management acceptability and scenic beauty will be explored as influenced by information about how the harvests are conducted and the long-term management intentions they might achieve. Such informed perceptions may prove more reliable indicators of eventual public opinions of New Forestry (Davidson et al. 1985). Some perceptions will be modeled against the corresponding vegetation structure of the pre- and post-harvest forests (Halpern et al. 1999), as has been done for forest types and management practices elsewhere in the U. S. (Ribe 1989). A diverse sample of respondents from Oregon and Washington will judge the photographs.

This Preliminary Study

As of this writing, the DEMO harvest treatments are not yet complete and are not photographed for inclusion in the main DEMO social perception study sketched above. This paper instead reports a preliminary study using photo-simulations to explore perceptions of forest landscapes that can inform the prospective main DEMO social perceptions study. This preliminary study focused on the minimum 15 percent green-tree retention harvests currently prescribed by the NFP rather than the broader range of retention levels in the DEMO study. Results from the larger DEMO study, including the social perceptions component, may affect current NFP retention standards (Franklin et al. 1997). It is timely to investigate the current NFP standard applied to national forest harvests, and this paper will focus on that.

Little research has considered the perceptions of New Forestry harvests or regeneration harvests prescribed by the NFP. The negative aesthetics of intensive harvests and clearcuts are well established (Ribe 1989). Studies indicate that less intense harvests, such as shelterwood cuts, thinnings, seed-tree retention cuts, smaller cuts, and patchy harvest patterns, can reduce the magnitude of adverse aesthetic reactions (Rutherford and Shafer 1969, Kenner and McCool 1985, McCool et al. 1986, Brunson and Shelby 1992, Schroeder et al. 1993, Palmer et al. 1995). Investigations that focus on the perceived acceptability of various intensities of harvest indicate that acceptability perceptions are complex, nuanced and probably more subject to the effects of information and respondents' attitudes than are more purely aesthetic perceptions (Vining 1992, Hansis 1995, Brunson and Reiter 1996). To the extent that perceptions of acceptability are more cognitive, i.e. involve thinking as well as reacting, they may conflict with aesthetic perceptions because ecologically functional attributes of forests, such as downed wood, dead trees, an understory, and burns, are often not viewed as beautiful (Benson and Ullrich 1981, Taylor and Daniel 1985, Ruddell et al. 1989, Nassauer 1992, Gobster 1996). The studies of perception of New Forestry harvests by Brunson and Shelby (1992) employed field visits by a small sample of respondents consisting mostly of university students. A larger, more diverse sample is needed to better investigate perceptions that might affect the politics

of public land management in the Pacific Northwest. This preliminary study (as well as the prospective main DEMO social perceptions study) employed such an improved sample.

This study investigated perceptions of aggregated versus dispersed 15 percent green-tree retention harvests. Simulated depictions of these two forms of regeneration harvest were shown to a sample of respondents along with corresponding depictions of clearcut and uncut forests. Respondents rated these scenes either for scenic beauty or acceptability. Half of the ratings of the 15 percent retention scenes were made with information about such harvests that might affect the ratings (henceforth, "informed ratings or scenes"). The other half were made without information ("uninformed ratings or scenes"). The average ratings for these informed versus uninformed regeneration harvest scenes were then compared to each other and to average uninformed ratings for uncut and clearcut versions of the same scenes.

The questions investigated were: (1) Are simple, uninformed perceptions of scenic beauty and acceptability of the green-tree retention harvest patterns different from those of conventional clearcuts? (2) How does information about the regeneration harvests affect perceptions of them? (3) Are dispersed retention harvests perceived as more acceptable than aggregated retention harvests, and do such differences change when ratings are made with information? (4) Are dispersed retention harvests perceived to be more scenically beautiful than aggregated retention harvests, and do such differences change when ratings are made with information? (5) Might differences in the scenic conditions of the harvests and their landscape context affect answers to any of these questions?

Methods

Scenery Sample

Two photographs of hillsides within the Mount Hood National Forest were used in the study, as shown at the top of Figures 1 and 2. These scenes were selected because they enabled production of high-quality simulations shown in the middle and bottom of Figures 1 and 2. Each occurred near similar views with recent harvests of known green-tree retention characteristics. Photographs of these nearby views, taken at nearly the same time of day and direction, were then used as imagery to make simulations that represented the 15 percent green-tree retention patterns as accurately as possible. Using only one photograph to simulate both dispersed and aggregated retention patterns would have better enabled comparing the ratings of the two patterns with no other confounding differences, such as other harvests or roads. However, the production of more valid simulations was judged more advantageous for this pilot study. Using two photographs also had the advantage of preventing respondents from detecting the same scene with different harvests. This detection might have affected their responses by causing them to guess what comparisons were the subject of the research. This might then have affected their responses differently than if they simply encountered the scenes in the field. Seeing different scenes with different harvests would be expected and more likely to produce judgments unaffected by survey procedures.

The simulation of an aggregated retention harvest minimally meeting NFP green-tree retention standards is depicted as the center image in Figure 1. It includes an aggregated patch of trees straddling an ephemeral stream channel. In the source imagery for the simulation that patch included about 15 percent of the timber volume that stood within the timber-sale area prior to harvest; the rest of the area was clearcut. Dispersed retention of trees was also simulated in the rest of the harvested area, consistent with NFP guidelines. These retention elements within the harvest unit were then simulated out of the image to produce the corresponding clearcut image at the bottom of Figure 1.

The image simulating a dispersed retention harvest is shown as the center image in Figure 2. This simulation was derived from imagery from a similar slope on which a dispersed retention harvest had recently been completed, retaining ten percent of the trees inside the harvest area. The simulation involved adding half-again as many retained trees within the harvested area. Then, to produce the corresponding clearcut image at the bottom of Figure 2, nearly all of these retained trees were simulated out of the image. The few trees left resembled recent clearcutting practices in the Mount Hood National Forest where a few trees are retained to anchor guy-wires for log-yarding equipment.

Figure 1. Aggregated retention scene set with uncut forest (top), simulated 15 percent green-tree retention harvest (middle), and conventional clearcut (bottom).

Figure 2. Dispersed retention scene set with uncut forest (top), simulated 15 percent green-tree retention harvest (middle), and conventional clearcut (bottom).

The two sets of images in Figure 1 versus 2 depict harvests of different size and stage of regeneration, different scenic contexts, and the presence (Figure 2) or absence (Figure 1) of other harvests. This difference allowed a preliminary exploration of potential confounding effects upon respondents' ratings of harvest size and stage of regeneration, as well as of other harvests in a scene. It was useful to explore the magnitude of these effects as they may influence perceptions of the diverse set of DEMO, YSS and LTEP harvests to be photographed for the main social perceptions study. (A more definitive analysis of these effects should occur through an analysis of covariance in this prospective, main study.) These scenic-contextual differences produced two scenic conditions as follows: One scenic condition, that might be expected to favorably affect scenic ratings, corresponded to the aggregated retention scenes (Figure 1). It included a smaller harvested area, early forest regeneration evident therein, and no other harvests in view. A second scenic condition, that might be expected to more adversely affect scenic ratings, corresponded to the dispersed retention scenes (Figure 2). It included a larger harvest, no forest regeneration evident therein, and two other harvests in view.

Preparation of Scene Surveys

The six study images (Figures 1 and 2) were made into color slides to be rated by respondents. They were placed among 54 other slides from the Cascade Mountains in Oregon and Washington as part of a larger "experience" of forest scenes for the respondents to simply see and judge. These included a wide variety of national forest scenes of various scales that depicted a diversity of landscapes from wilderness to heavily managed vistas. This approach sought to elicit ratings indicative of judgments that might be made upon encountering the scenes during trips through the forest, as opposed to the more intentional judgments that might be made if attention were focused on just the subject scenes with their obvious comparative content. The 15 percent retention slides were rated both with and without information, so second copies were placed among other sets of slides that were shown to respondents with corresponding one-sentence information statements. Together, these formed a shorter, 15-slide "guided-tour experience" of diverse national forest scenery that followed the first, uninformed "experience" during the rating sessions.

The study slides were placed into two slide trays as illustrated in Figure 3. (Two trays were needed to include all the slides for this and another study.) Each tray was shown to different respondents, roughly half of whom rated its slides for scenic beauty and half for acceptability (Figure 3). The 15 percent retention slides were placed into the trays so that each respondent rated one retention pattern without information and the other pattern with information (Figure 3), without having his/her rating affected by an awareness of a repeated scene with information the second time. The 15 percent retention slides involved in this designed allocation were randomly placed within the required sections of the two trays. The other study slides were randomly placed within the slide trays' uninformed sections (Figure 3).

When the informed slides were shown to the respondents, one and the same information statement accompanied both the aggregated and dispersed retention simulation slides for rating both acceptability and scenic beauty. It was: "This harvest left 15 percent of the living trees standing as future habitat and a way of helping the ecosystem reestablish itself as a new forest grows back there." This statement was constructed to be simple but indicative of how the harvests might be perceived differently from commonplace clearcuts. It sought to capture the essence of New Forestry and the harvesting prescriptions found in the NFP, particularly regarding retention of biological legacies. At the same time, it sought to be relatively objective to reduce the extent to which it would produce its own affect independent of the appearance of the scenes (Brunson and Reiter 1996). The words "harvest," "ecosystem" and "habitat" do have such affective tendencies (Kellert 1983), but were used anyway, after deliberation, as necessary to express the needed content.

Respondent Sample

Members of a variety of organizations rated the slides as a special activity during their regular meetings. They filled in a questionnaire and rated slides privately, anonymously and independently on individual rating forms, as described below. Groups were recruited to capture a diversity of people with active interests in preservation versus

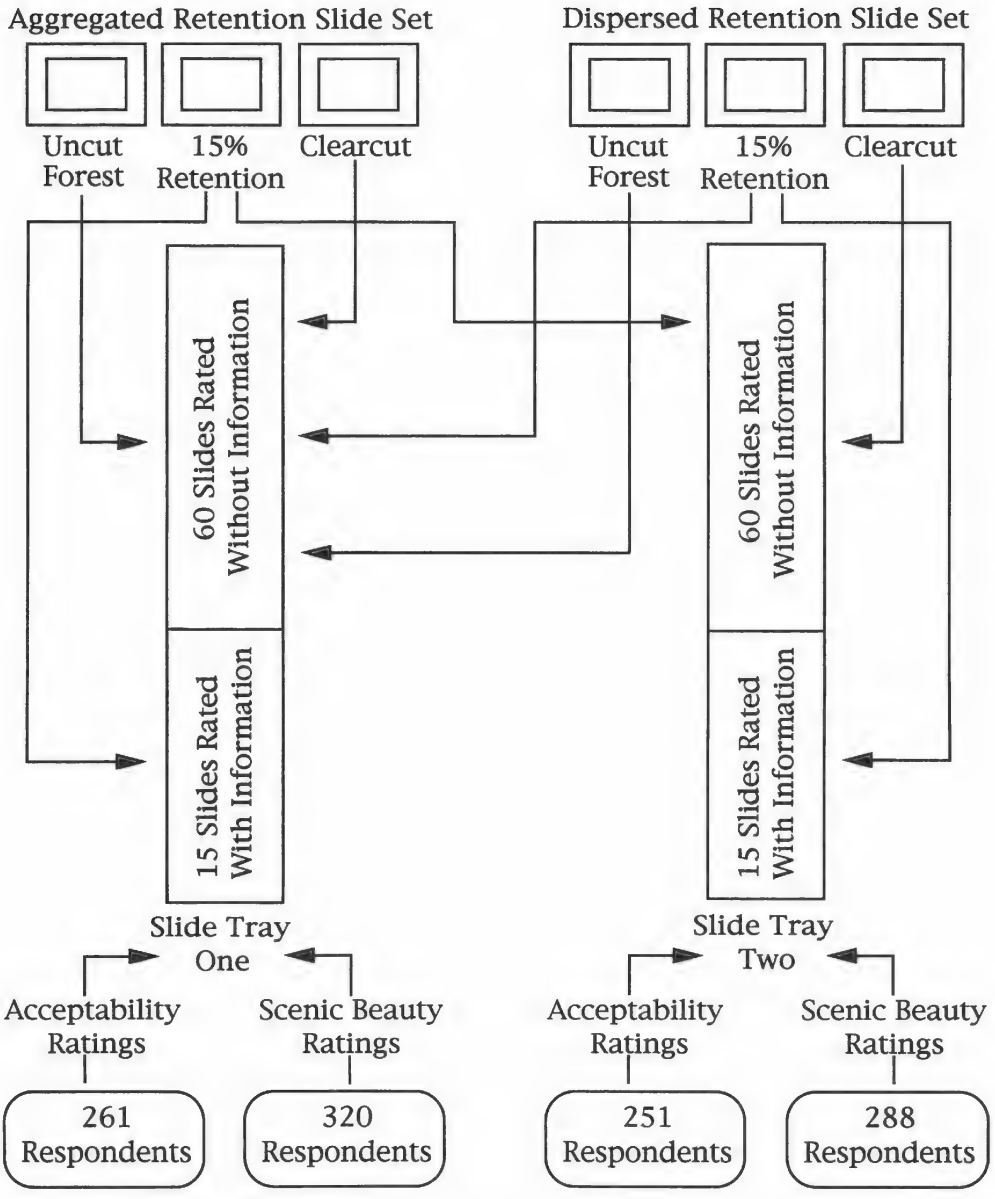

Figure 3. Relationship between the study scenes, whole slide sets that were rated, and respondent sets that rated slides for different qualities.

commodity production on public lands (Chandler and Lee 1994). They were also recruited to include a variety of rural, suburban, and urban respondents throughout western Washington and Oregon to represent the diversity of attitudes toward land management found across such places (Tichenor et al. 1971, Tremblay and Dunlap 1978, Lyons 1983). To a lesser extent, diversity was sought in incomes, ages, educational attainments, relationship to the forest product industry, and recreational preferences. The groups included natural-resource-related organizations such as logging and property rights advocates, environmental groups, civic clubs, social clubs, professional organizations, outdoor recreation groups, higher-education classes, business clubs, corporate offices, granges, and neighborhood associations.

Each group of respondents viewed one of the two slide trays and rated its slides for either acceptability or scenic beauty. The respondent groups needed to be allocated to the judgment of these two qualities. At first, combinations of a slide tray and quality to be judged (scenic beauty or acceptability) were assigned to each group at random until all four combinations had been administered to at least 200 respondents. From that point on groups were assigned intentionally to make the four sets of respondents who rated each of the combinations "similar" to each other to reduce the probability that any one would have a chance over-representation of respondents with a key bias. Groups were judged to be similar if each contained at least one fourth residents of rural areas and cities with populations less than 20,000, and if each contained roughly equal numbers of respondents tending to favor forest production versus forest protection. For this latter purpose, a running tally was kept of responses to two questions about the northern spotted owl controversy. These were questions that asked how much respondents agreed or disagreed with statements. The first statement was that the spotted owl should be saved even at a high economic cost, and the second was that the spotted owl should be saved only if it can be done without infringing on private property rights. This intentional assignment of groups was to continue until at least 1,000 respondents were sampled. It was necessary to exceed that number to achieve the rough similarity sought among the combinations of slide trays and qualities judged. A total of 1,120 respondents from 57 groups were surveyed: 18 groups (261 respondents) rated the slides in tray one for acceptability, 17 groups (320 respondents) rated tray one for scenic beauty, 8 groups (251 respondents) rated the slides in tray two for acceptability, and 14 groups (288 respondents) rated tray two for scenic beauty (Figure 3).

Slide Rating Surveys

At the outset of the slide rating sessions, all respondents were instructed to make their uninformed judgments based upon the "knowledge and sensibilities they already had." They were told to view the slides as scenes they might encounter traveling through national forests in the Cascade Mountains "distant from home" and "distant from their favorite place to visit" in those mountains. Those who rated slides for acceptability were instructed to rate the landscape in each slide for the "acceptability of its condition as a publicly owned and managed national forest." They were instructed that they could base these judgments on the appearance of the landscape and/or their awareness of the causes of its condition; the purposes of the management that produced the landscape and/or alternatives to that management; the feasibility of those options and any unknowns and risks involved that they knew of; or anything else they wished (Brunson 1993). They rated each numbered slide on a scale from minus five for very unacceptable to plus five for very acceptable, with zero assigned to slides for which they felt either neutral or undecided.

The respondents participating in scenic beauty sessions were simply instructed to rate the slides for "scenic beauty." Studies indicate that this is the only description needed to instruct ratings of scenic beauty (Zube et al. 1982, Hull et al. 1984). Respondents rated scenic beauty on the same numeric scale as was used for rating acceptability, except that they were instructed that the scale ranged from "very ugly" to "very beautiful," with zero assigned to slides they found neither beautiful nor ugly or for which they were undecided.

Immediately after the respondents rated the 60 slides either for acceptability or scenic beauty, another rating session began for 15 more slides rating the same quality and using the same scale as before. In this new session, each slide was accompanied by a sentence containing information about the landscape it depicted. This sentence was both spoken while the slide was displayed and provided on the response forms in large print

just above the rating scale for the corresponding slide number. Respondents were instructed to wait until after the information sentence had been read before making their ratings.

Data Analysis

Data were analyzed by examining the patterns of average ratings (Schroeder 1984) for one quality at a time and within one scene set at a time, i.e. comparing the scenes in Figure 1 or those in Figure 2. T-tests were used to test for statistically significant differences (alpha =.01) between pairs of average ratings (Table 1). This small alpha value was used to reduce the chance of spuriously identifying a statistically significant result given the numerous comparisons performed. Paired t-tests were used to compare average ratings generated by the same sets of respondents. Unpaired t-tests were used to compare average ratings generated by different respondent sets.

The aggregated versus dispersed retention results came from different slide sets, each with its own scenic context and reference slides depicting uncut and clearcut forests (Figures 1 and 2). This made comparing the average ratings for the two different retention patterns problematic and tentative. However, to facilitate a graphic comparison for this preliminary study, a standardization of these average ratings was made. This was a linear range transformation to a common numeric scale. This transformation set the average rating for the clearcut slide to zero and the average rating for the uncut forest to 100. The transformed average ratings for the green-tree retention harvests then fell proportionally between. This enabled a rough comparison of the average ratings for the two retention patterns versus those for clearcut and uncut forests.

Results

Average rating values and the corresponding transformed values appear in Table 1 with the t-tests used to compare average ratings within the sets of comparisons depicted graphically in Figures 4 and 5. As might be expected, within the scene sets for both the aggregated and dispersed retention patterns, the clearcut scenes exhibited the lowest average ratings and the uncut forest the highest. The average ratings for the green-tree retention harvest scenes fell in between or were statistically equivalent to the clearcut.

There was not a statistically significant difference between the average acceptability ratings of the uninformed clearcut versus the uninformed regeneration harvest in either slide set (Table 1). The same held true in comparing the average scenic beauty ratings for the clearcut and the uninformed dispersed retention harvest (Table 1). In contrast, the average rating of scenic beauty for the uninformed aggregated retention harvest scene was significantly greater than that of the corresponding clearcut scene (Table 1, Figure 4).

The information statement had a significant and substantial positive association with a change in average acceptability ratings for both retention patterns (Table 1, Figures 4 and 5). However, the information statement was evidently much less influential upon average ratings of scenic beauty. Information was not significantly associated with a change in the average scenic beauty rating of the aggregated retention slide (Table 1, Figure 4). Although the average scenic beauty rating of the dispersed retention slide with information was significantly greater than that without information (Table 1, Figure 5), this difference was smaller than that observed for the acceptability ratings (Figures 4 and 5).

The transformed average acceptability ratings at the top of Figure 6 suggest that the aggregated retention harvest was perceived as slightly more acceptable on average than the dispersed retention harvest, with or without information. The comparison of transformed average scenic beauty ratings at the bottom of Figure 6 is much more suggestive of a difference. There, the average ratings for the aggregated retention pattern are higher than those for the dispersed retention pattern. These differences are much greater than those associated with informed versus uninformed scenic beauty ratings within either slide set (Figure 6).

The differences in scenic content between the scene sets in Figures 1 versus 2 may be associated with differences in the average ratings produced from those scene sets. The aggregated retention slide set, with smaller harvest sizes, more sapling regeneration evident within its harvests, and no other harvests in view, produced average ratings greater than zero for both judged qualities (Figure 4). In contrast, the dispersed harvest slide set, with larger simulated harvest size, no sapling regeneration evident, and other harvests in view, produced average ratings across a wider,

TABLE 1. Matrices of t-tests for all comparisons of mean ratings within each combination of retention pattern seen and quality judged. The top row of each matrix indicates mean rating values with corresponding transformed mean rating values in parentheses.

	Uninformed Clearcut	Uninformed 15% Retention Harvest	Informed 15% Retention Harvest	Uninformed Unharvested Forest
Acceptability of Aggregated Retention Scene Set				
Mean Ratings	1.08 (0)	0.99 (-6)	2.13 (64)	2.71 (100)
Uninformed Unharvested Forest	t = 11.15 p < 0.001 df = 260	t = 8.68 p < 0.001 df = 250	t = 3.41 p < 0.001 df = 260	
Informed 15% Retention Harvest	t = 6.85 p < 0.001 df = 260	t = 5.51 p < 0.001 df = 250		
Uninformed 15% Retention Harvest	t = 0.78 p = 0.43 df = 250			
Scenic Beauty of Aggregated Retention Scene Set				
Mean Ratings	0.80 (0)	1.68 (67)	1.72 (71)	2.11 (100)
Uninformed Unharvested Forest	t = 11.17 p < 0.001 df = 319	t = 3.08 p = 0.002 df = 287	t = 3.09 p = 0.002 df = 319	
Informed 15% Retention Harvest	t = 7.73 p < 0.001 df = 319	t = 0.34 p = 0.73 df = 287		
Uninformed 15% Retention Harvest	t = 5.04 p < 0.001 df = 287			
Acceptability of Dispersed Retention Scene Set				
Mean Ratings	-1.79 (0)	-1.65 (4)	0.00 (54)	1.53 (100)
Uninformed Unharvested Forest	t = 13.29 p < 0.001 df = 250	t = 17.11 p < 0.001 df = 260	t = 6.26 p < 0.001 df = 250	
Informed 15% Retention Harvest	t = 8.62 p < 0.001 df = 250	t = 5.83 p < 0.001 df = 250		
Uninformed 15% Retention Harvest	t = 0.78 p = 0.43 df = 250			
Scenic Beauty of Dispersed Retention Scene Set				
Mean Ratings	-1.38 (0)	-1.28 (3)	-0.49 (28)	1.77 (100)
Uninformed Unharvested Forest	t = 15.06 p < 0.001 df = 287	t = 20.53 p < 0.001 df = 319	t = 10.43 p < 0.001 df = 287	
Informed 15% Retention Harvest	t = 5.25 p < 0.001 df = 287	t = 3.39 p < 0.001 df = 287		
Uninformed 15% Retention Harvest	t = 0.52 p = 0.60 df = 287			

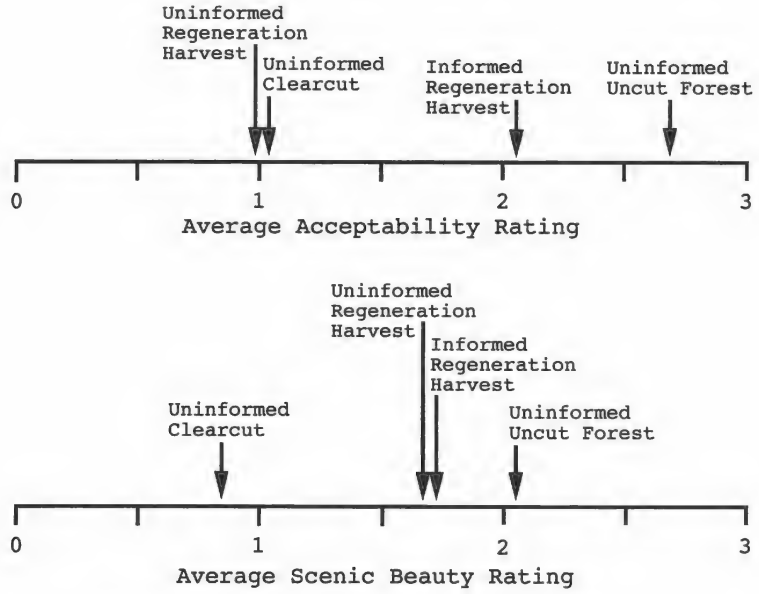

Figure 4. Distribution of the average ratings for aggregated retention scene set.

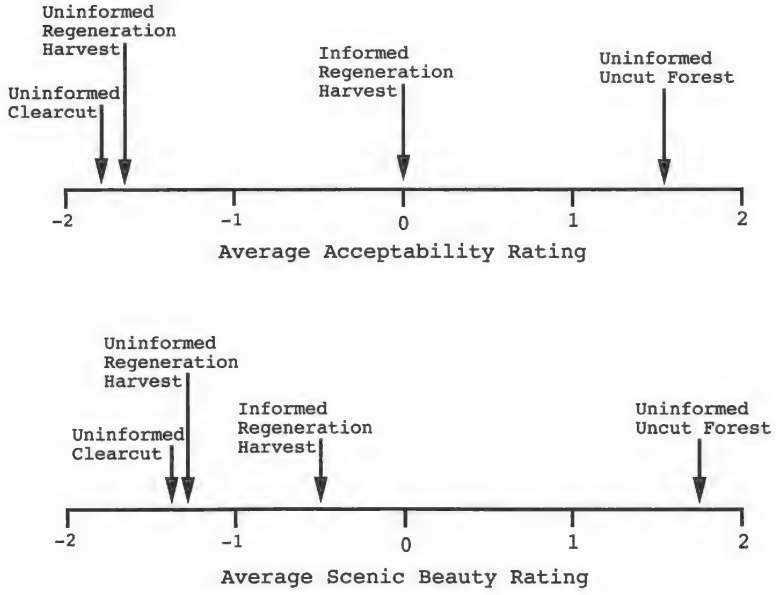

Figure 5. Distribution of the average ratings for dispersed retention scene set.

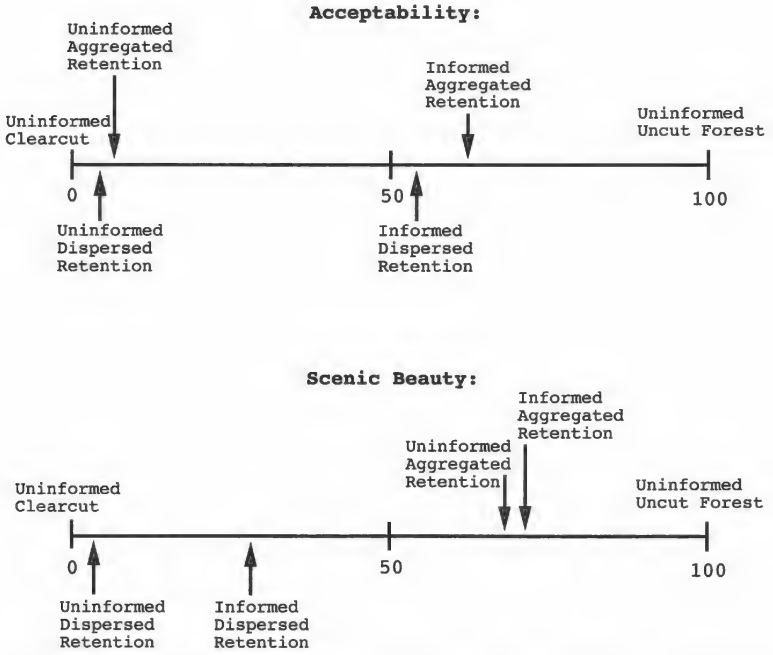

Figure 6. A comparison of transformed average ratings of aggregated versus dispersed green-tree retention harvest scenes.

positive and negative, range. There, the simulated harvest scenes elicited non-positive average ratings for acceptability and scenic beauty, while only the uncut forest scenes' average ratings were positive for both judged qualities (Figure 5).

Discussion

This pilot study used a few scenes comparing different green-tree retention patterns in harvests of different sizes and set in different scenic contexts. It lacked the many replications in controlled visual contexts and the variety of retention levels planned for the main DEMO social perceptions study. These limitations permitted only a simple set of statistical, pairwise comparisons supplemented by graphical analysis. Interpretation should therefore be considered preliminary. Nonetheless, managers and policy makers can make use of these preliminary findings as the best currently available information awaiting larger, more definitive studies.

When perceived simply, with no information or knowledge about New Forestry, 15 percent green-tree retention harvests are not likely to be perceived as any more acceptable than traditional clearcuts. However, information about the nature and intentions of New Forestry evidently can have a positive influence upon perceptions of the acceptability of these NFP-style retention harvests. The perceived acceptability of regeneration harvests is evidently the same between the two patterns of retention compared in this study, whether or not information about New Forestry is provided.

Uninformed perceptions of the scenic beauty of 15 percent green-tree retention harvests evidently may also be similar to those of conventional clearcuts, as in the case of the dispersed retention harvest in this study. An exception occurred when the pattern of retention was aggregated so as to break the harvest unit up into smaller openings that maintain more forest canopy continuity in vista views. Such harvests can be perceived as more beautiful than clearcuts. In this

study, the aggregated retention harvest was viewed in the context of no other harvests, while the dispersed retention harvest's vista included two other, older clearcuts. Further research is needed to see how influential such scenic context factors are upon perceived scenic beauty in relation to the influence of adding retention harvests to landscapes.

Information about New Forestry appears much less associated with changes in perceptions of scenic beauty than was evident for perceptions of acceptability. This is consistent with theoretical suggestions of how such perceptions should differ (Ittelson et al. 1976), and with differences suggested by other studies (Simpson et al. 1976, Russell et al. 1981, Tips and Savasdidara 1986, Pukkala et al. 1988, Dearden 1989). An exception was found for the larger, dispersed-retention harvest in this study. There, information evidently increased perceptions of scenic beauty somewhat, perhaps because of interaction between the content of that scene and the affective words included in the information statement. More research is needed. Information has been found to enhance perceptions of scenic beauty, but usually when it indicates that landscapes are "natural" or "healthy" and/or are of a status that implies scenic or "natural" value (Carls 1974, Hodgson and Thayer 1980, Anderson 1981). But, such effects have not been observed for information identifying different kinds of "unnatural" forest management like harvests. This, and the lack of a substantial, reliable association between information and scenic beauty perceptions in this study and others (Brunson and Reiter 1996), suggests that such perceptions might best be enhanced by improving the appearance of regeneration harvests rather than by education or information.

No differences in average ratings were large enough to suggest that dispersed retention patterns may be perceived as more or less acceptable than aggregated patterns at the 15 percent harvest retention level, whether or not information was provided.

Aggregated retention was evidently perceived, on average, as more scenically beautiful than dispersed retention patterns, irrespective of whether either one or both perceptions of the two retention patterns were informed. Thus, aggregated retention may be the decisively preferable scenic pattern at the 15 percent retention levels studied. The reasons may be the same as those discussed above regarding the superiority of the aggregated retention pattern compared to clearcuts.

This pilot study did not separate the effect of retention pattern from that of scenic-context conditions. Coincident variation between these two factors suggests some caution in interpreting the results. The aggregated retention pattern was found to be more beautiful, and, the scenic conditions of the aggregated retention slide set elicited a narrower range of only positive ratings of scenic beauty (and acceptability). This suggests two possible interpretations: (1) If the scenic conditions had been identical between the two harvest patterns, the difference in perception of scenic beauty between the aggregated and dispersed patterns may have been smaller, as suggested by the bottom of Figure 6. However, it is likely that the difference would still have been notable given the strong contrast in ratings of scenic beauty and acceptability for the same comparison of scenic conditions (top of Figure 6). (2) The lack of an association between information and differences in perceived scenic beauty for the aggregated retention scene may be due, in part, to the fact that most respondents chose to rate that scene using only the narrower, positive part of the rating scale. This would have compressed the two average ratings, with and without information, for that scene. This compression did not occur for the dispersed retention scene because the respondents rated it using a wider range of positive and negative values. Hence, a difference associated with information could more readily emerge. The strength of the association between levels of perceived scenic beauty and information about New Forestry therefore remains uncertain.

Conclusions

The trade-offs between negative public perceptions and silvicultural benefits of clearcuts is a long-standing dilemma in forest management (Horwitz 1974). This study sheds new light on whether vista views of the 15 percent minimum retention standard now prescribed by the Northwest Forest Plan might offer some resolution. The results are not very encouraging. It appears likely that any pattern of 15 percent retention will not be seen by naive viewers as any more acceptable than clearcuts. If the green-trees retained in harvests are dispersed, then naive viewers will find them no more scenically beautiful than clearcuts.

Some resolution to the perception of timber harvests is offered if observers are educated about the nature and intentions of green-tree retention forestry. This may be particularly true of people who have a vested or ideological interest in forest management and who tend to judge harvests on more than their aesthetic appearance. The more purely aesthetic judgments of recreationists and those just passing through the forest, with little or no vested or ideological interest in forest management, may be less influenced by education.

Scenic beauty perceptions may instead be improved if the aggregated clumps of retained trees are designed to minimize the visual magnitude (Iverson 1985) of openings in the forest canopy. Retention at levels greater than 15 percent may also improve scenic beauty perceptions for either or both aggregated and dispersed retention patterns, and may do likewise for perceptions of acceptability. Future DEMO social perceptions research will investigate this further.

This study suggests that information about forest harvests can influence perceptions of scenes including such harvests. This demonstrates that some perceptions of harvests can assimilate both what is seen and the cognitive content thereof. This suggests that when managers seek to optimize the social acceptability of forest practices they should pay attention to more than appearance. Instead, they should seek to integrate the appearance and content of the landscapes they manipulate. This could be consistent with ecosystem management decision making where the "appropriateness" of landscapes, as proposed by Gobster (1996) or Tlusty (1992), rather than just their appearance, is the main objective. Such an integrated approach might produce more socially acceptable forest landscapes than the less perceptibly sensible landscapes that arise from traditional, reductionist planning where each resource, including visual quality, is separately understood and competitively sub-optimized (Kimmins 1992, Hirt 1994).

Acknowledgements

The author thanks the members of the DEMO, LTEP, and YSS research teams for their support and advice. Particular thanks go to Paul Gobster, Mike Amaranthus, Jim Palmer, Sally Schauman, Susan Bolton, Charles Halpern and two anonymous reviewers for their valuable assistance. This is a product of the Demonstration of Ecosystem Management Options (DEMO) study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources. Substantial support has been provided by the USDA Forest Service, North Central Research Station.

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The Benefits and Challenges of Large-scale Silvicultural Experiments: Perspectives from Forest Managers on the Demonstration of Ecosystem Management Options (DEMO) Study

Abstract

The purpose of this paper is to share with other land managers and scientists some of the lessons learned in implementing the Demonstration of Ecosystem Management Options (DEMO) study, and to give our perspectives on the application of large-scale harvest experiments on public lands. We briefly discuss aspects of site selection; timber sale planning, administration, and post-harvest activities; assistance in study installation; funding and timelines; and public involvement. We offer perspective on large-scale studies, including the importance of adaptive management, the value of a study plan, the necessity for collaboration in the process, and the benefits of public involvement.

We have already learned a great deal about implementing large-scale experiments, gathered a wealth of information about the DEMO research sites, and experienced first-hand the challenges and rewards of collaboration among scientists and managers. Perhaps the most important lesson to emerge is that the rigidity required of scientific study may conflict with operational forest management. However, collaboration among participants can allow implementation of large-scale experiments that are both rigorous in design, and relevant in practice. Managers and scientists involved with the DEMO study would like data collection and analysis to continue in future decades. Knowledge of long-term responses, such as tree growth and forest structural development, will not be developed in the short run. We would also like to encourage new studies within the existing research sites, timely sharing of research results, and continued collaboration among scientists and managers.

Introduction

Forest managers on public lands are faced with the challenge of implementing ecosystem management. A key feature of ecosystem management is the concept of adaptive management, a process by which we test ongoing standards and practices, and accordingly revise management practices. The Demonstration of Ecosystem Management Options (DEMO) study will test an important component of the Northwest Forest Plan (USDA and USDI 1994)—the requirement of green-tree retention during regeneration timber harvests.

The DEMO study is being implemented on eight sites in western Oregon and Washington, on public lands managed for commodity production and other resources. Installing a large, multi-disciplinary experiment on managed lands has proven challenging for both managers and scientists. It has, however, been a rewarding endeavor; the study has resulted in increased collaboration, has already provided new information, and has been a valuable learning tool for both managers and scientists. The goals of this paper are two-fold: (1) to share with other managers and scientists who may embark on similar large-scale experiments, some of the lessons that we have learned, and (2) to give our perspective on the values of DEMO and other large-scale research on public lands.

Lessons from Project Implementation

The DEMO study is a large-scale experiment that focuses on the effects of different levels and patterns of green-tree retention on various elements of Pacific Northwest forest ecosystems. These include responses of wildlife, vegetation, fungi, and canopy invertebrates; effects on snow hydrology; social perceptions of these harvests; and harvesting costs (Aubry et al. 1999). Each of the eight replications, or blocks, in the study include six 13-hectare (32 acre) treatments:

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1. 100% retention (uncut control)
2. 75% retention (harvest in small, 1-ha circular patches)
3. 40% dispersed retention (retained trees uniformly dispersed)
4. 40% aggregated retention (retained trees in five, 1-ha circular patches)
5. 15% dispersed retention (retained trees uniformly dispersed)
6. 15% aggregated retention (retained trees in two, 1-ha circular patches)

Four DEMO replications are located in western Oregon on the Umpqua National Forest. Four replications are in western Washington—three on the Gifford Pinchot National Forest and one on Washington State Department of Natural Resources (DNR) land (see Figure 3 in Aubry et al. 1999).

The DEMO study has presented numerous challenges, due in large part to different objectives and working approaches between research and management (see also Franklin et al. 1999). Researchers must be concerned with evaluating treatment effects in an objective, unbiased fashion. These concerns have required harvests that may be more uniform in treatment and arrangement than managers would otherwise implement. In addition, treatments must be randomly assigned to experimental units rather than in some manner that optimally meets management objectives. These requirements have led to rather unconventional approaches to timber sale planning, preparation, administration, and post-sale operations in implementing the DEMO study treatments.

Constraints of the Study Design on Site Selection

One of the biggest challenges with implementing the DEMO study was finding suitable sites for the treatments. The experimental design required relatively large, uniform, regularly shaped units that were difficult to find on the managed landscape. Site selection required efforts from both scientists and managers to ensure that experimental needs were met, while minimizing adverse environmental effects from implementation of the timber harvests. Several criteria, in combination, made site selection difficult:

- The DEMO study design required relatively large units. Each unit had to be 13 ha (32 acres) in size, large enough to encompass the home ranges of small mammals (see Aubry et al. 1999).
- Units had to be square or slightly rectangular in shape, to conform to the shape of the sample grid, and to maximize interior habitat. Many potential sites were large enough, but lacked enough length or width to include the entire 13 ha grid.
- Sites had to be composed of upland, mature forests, the more homogeneous the better. Streams, riparian areas, roads, and existing harvest units were to be avoided if possible, to reduce additional sources of variability.
- The experiment had to be implemented on lands available for timber harvest in current Forest Plans.

Given these criteria, National Forests found it difficult to locate suitable sites. The mosaic of existing harvests, roads, and streams made it difficult to place 13 ha square units within landscapes that lacked these features. The most limiting factor proved to be streams; we found very few areas where replications could be placed without impacting even intermittent streams. Lands allocated to timber harvest amount to approximately 18% of the Gifford Pinchot National Forest, and 25% of the Umpqua National Forest, which also limited areas available for site selection.

Two changes to the experimental design and its siting made implementation possible. First, an early design called for eight treatment units (see Franklin et al. 1999), each 20 ha or larger; decreasing the number of treatments to six and reducing the size to 13 ha, helped considerably. The reduction in size was a compromise from the more ideal size originally proposed for arboreal rodent sampling (Lehmkuhl et al. 1999). Second, the Washington DNR was contacted and agreed to install one of four replications in Washington (Capitol Forest). Although it was not difficult for the DNR to find suitable harvest locations, there was concern in the organization that they not commit adjacent lands to serve as buffers (a similar concern exists with National Forests). Thus, we found that we could locate suitable sites, but only with difficulty, after revisions to the study design and by finding another cooperator in Washington (DNR). Studies of similar size and scope will be increasingly difficult to establish on National Forest lands. Smaller, more

focused studies will be easier to install and implement, although it may not be possible to ask questions that require sampling at larger spatial scales.

Timber Sale Planning, Administration, and Post-harvest Work

Environmental Consequences of the Treatments

Requirements of the DEMO study presented unique challenges for timber sale planning. Planners typically design harvest units to minimize adverse environmental and social impacts, to meet the standards and guidelines of National Forest Plans, or to fit in with harvest schedules on DNR lands. The DEMO experimental design imposed several constraints. Two examples illustrate this problem. First, in replicated experiments, treatments must be randomly assigned to avoid investigator bias. This requirement precluded the possibility of applying treatments with higher levels of green-tree retention to the more environmentally or socially sensitive sites. Second, the design required uniform application of treatments to minimize variation: patches retained in aggregated retention treatments had to be of equal size and distance from each other (see Aubry et al. 1999). If streams were present within units, the design required that riparian areas along those streams be harvested, except where they occurred within uncut patches. In essence, the study design did not accommodate the use of streamside buffers, or "riparian reserves" which are prescribed in the Northwest Forest Plan. These buffers would have had a confounding influence on the primary treatment effects. Managers were faced with a design that increased the probability of adverse environmental consequences, and that allowed only limited ability to work within the design to minimize environmental consequences.

Other specific environmental concerns included the locations of some treatment units within home ranges of northern spotted owls, or in habitat for threatened anadromous fish. These situations required consultation with US Fish and Wildlife or National Marine Fisheries Service biologists, to determine the potential effects of the proposed timber sales on these species. One Oregon replication is located within a municipal watershed which has earthflow terrain and soils with colloidal clays. The Environmental Protection Agency (EPA) reviewed the proposed timber sale and the research design and was concerned that in two treatment units, the removal of trees within riparian zones could increase stream turbidity over both the short and long term. EPA, managers, and scientists agreed to mitigate these concerns by providing additional large woody material to the streams. Some trees will be felled into streams, while others will be killed and left standing, to fall into streams over the next several decades. The additional woody material in the streams should help to trap sediment, but will have minimal effect on the upland processes that are being studied.

Logging Systems

The logging systems used in the DEMO study are often non-standard and more costly, due to requirements of the study design. To minimize additional sources of variation it was required that the same logging system was used in all treatments within a block. This led, in some cases, to cable or helicopter logging of gentle topography, where ground-based systems might otherwise have been used. An exception was permitted at the Capitol Forest block, where due to a combination of steep and gentle topography, the use of a single system would have led to greater variation in disturbance. Here, a combination of logging systems was used.

A secondary consequence of study constraints on logging systems was that it affected our ability to analyze the harvest costs of the different treatments. Because different logging systems are being used in different blocks, there was little opportunity for comparison between blocks. In addition, some non-standard operating procedures were employed, such as yarding tops to reduce slash. This measure served to remove slash in a very uniform manner, which was beneficial to many aspects of the study; however, it added a non-standard cost, adding to the difficulty in analyzing costs of operations. As a consequence, a harvest cost study was discontinued after the first two blocks were harvested.

Sale Preparation and Administration

Sale preparation activities were largely straightforward, but some tasks were more labor intensive than for standard sales. For example, the experimental design required that the basal area

of trees left in the dispersed retention units was within five percent of that in the corresponding aggregated retention unit (Aubry et al. 1999). This required more intensive tracking of marked trees in the dispersed retention units than under normal marking operations. Layout of harvest or non-harvest areas within treatment units also required different techniques, often taking more time than standard layout procedures. Extra time was often required to best place DEMO units, with their exact size requirements, on the landscape between streams and other features. On the other hand, once the sampling grids were surveyed and in place, they helped to make some layout work easier. Interior grid points could be used to locate within-unit harvest or retention patches.

The study design also required non-standard contractual provisions. For example, contractual language was included that required sale purchasers to collect information for preliminary studies of harvesting costs. Provisions were also included to protect sampling-point designation tags from damage due to logging operations. Standard provisions allowing for possible sale extension due to market conditions were withdrawn from sale contracts, because harvest delays could introduce unwanted temporal variation in treatments and the sampling units thereof. These provisions added complexity to the timber sales, and probably affected their marketability.

Since DEMO timber sales were non-standard, extra efforts were made to inform prospective purchasers about the project. During sale advertisement, meetings and field trips were held with prospective purchasers to discuss study requirements and research objectives. Meetings were also held with sale purchasers prior to harvest, again to clarify the intent of the experiment. These meetings were very helpful; requirements that at first appeared unusual to purchasers made more sense once the underlying objectives were understood.

In general, the potential environmental consequences of DEMO timber sales proved more difficult to assess than do those of most sales. Despite reduced flexibility to mitigate for potential consequences, we did not encounter significant adverse effects. The logging methods used were sometimes not standard, affecting the harvest cost study. Sale preparation and administration were fairly straightforward; the outcome of harvests to date illustrate the importance of clear communication with timber operators.

Post-Harvest Activities

Post-harvest practices, such as slash disposal, snag creation, and reforestation will be treated somewhat differently in DEMO study areas than in normal timber sales, once again to minimize confounding effects. Regeneration harvests on National Forests usually contain provision to create snags, by topping and killing "wildlife trees", green trees retained for that purpose. This measure mitigates the loss of snags from timber harvest, due to statewide safety regulations that require snags to be felled during harvest operations if they present a safety hazard. Normally, some wildlife trees are killed immediately after timber harvest, while others are left alive, to be topped in future years or to eventually become snags through natural mortality.

Because the principal effects being tested in the DEMO study are the pattern and amount of green-tree retention, leaving additional green trees for eventual conversion to snags could have confounding effects. Scientists and managers agreed to leave 6.5 additional green trees per hectare, provided that they were uniformly distributed and converted to snags immediately after harvest. This allowed for some mitigation of the loss of snags, while not further confounding the main effects of retention.

Slash disposal operations will also be affected by the study design on some blocks. Researchers seek uniform methods of slash disposal among harvest units; the goal is to minimize slash treatment, but provide for fuel reduction and allow for adequate sampling of post-harvest communities. Possible approaches include no treatment, yarding tree tops to landings along with logs, and slash piling.

On some blocks, contingency plans were made for additional slash treatment (burning) if initial approaches were inadequate. Decisions to pursue these options will be made by managers and scientists following harvest. From an experimental perspective, additional work is not desirable; it may add variability among treatments and delay initiation of post-harvest sampling. On the first two blocks harvested, slash levels were acceptable following the initial treatment (yarding tops). For one of these, managers would have preferred

to have greater slash removal, but could accept the levels present.

In summary, we found that the DEMO study design resulted in timber sales that were more difficult to plan and implement than standard timber sales. However, we also discovered that we have the flexibility to work with scientists to design and implement large-scale experiments on our matrix lands.

Assistance in Study Installation

The National Forests and Washington DNR not only prepared and sold the DEMO-related timber sales, but also installed the study sampling grids and provided logistical assistance to data collection efforts. Each DEMO treatment unit contains a grid of permanent sampling points, used to structure data collection (see Aubry et al. 1999). The National Forests and DNR were asked to establish the sampling grids. Engineering personnel were able to utilize survey techniques to meet the tight measurement tolerances required by the study design. The effort was costly (about $3,000-$5,000 per block) and there were a few communication problems regarding installation criteria on some blocks. Overall, however, the effort represented an excellent use of resources; during this period (1993-94) National Forest engineers had relatively low workloads due to a court injunction limiting timber harvests in spotted owl habitat, and they had the right skills to accomplish the job. It also had a secondary benefit, enabling engineers to contribute to a forest research project, something they may not normally have the opportunity to do.

National Forest and DNR managers were also confronted with additional logistical challenges: helping to secure housing or camping sites for university field crews, providing access and maps to study sites, occasionally arranging for volunteer assistance for researchers, and helping to coordinate the timing of field activities. As a consequence, National Forest and DNR personnel have become more familiar with the study and with the university researchers involved.

Funding and Timelines

Court injunctions, timing and processing of funds, and annual budgeting affected initial implementation of the study. A first appropriation of $1.5 million was allocated in fiscal year 1993, an amount that did not arrive on the National Forests until May (seven months later). At that time, National Forest lands within the range of the northern spotted owl were enjoined from harvests in spotted owl habitat, and a plan to address that injunction was being formulated. Thus, it was unclear when it would be possible to implement the DEMO study. Draft plans for the study were prepared and a "pilot" effort was begun on the Umpqua National Forest, with some data collection accomplished by Forest Service personnel during fall 1993. Additional replications were established, and pre-harvest data collection (by participating Universities under cooperative agreements) began in 1994. A study plan was developed and completed in 1996. The pilot data, collected before study plans were developed were never used. The completion of the Northwest Forest Plan (USDA and USDI 1994) allowed for completion of timber sale plans on National Forest blocks, and the study has progressed in a relatively smooth manner since then. However, based on our experience, a more efficient avenue for study development would have been to fund completion of a study plan first, then to implement the study.

Annual budgeting has also made planning difficult. Recently, the Pacific Northwest Research Station and the Pacific Northwest Region signed a memorandum of understanding helping to ensure 4 years of funding for the first phase of post-harvest analysis.

Public Involvement

The DEMO study has presented some interesting challenges in public involvement. Both managers and scientists participated in many meetings describing the rationale for the study, the study questions being asked, and the information being collected. Many people expressed interest in the study. Some were concerned about potential impacts of the timber sales, and others wondered whether the Forest Service would continue the research once the trees were harvested. Modifications to the study plan reduced probable environmental impacts (e.g., reducing the number and size of units, dropping an initially proposed clearcut treatment, and other smaller changes). These modifications to the design were at least partially in response to feedback gathered during public involvement.

Perspectives in Implementing Large Harvest Experiments

The DEMO study is still in its implementation stage, with initial post-harvest analysis several years in the future. However, we have learned a great deal about the benefits and potential problems involved with installing large-scale harvest experiments on managed National Forest and State lands. The study has been difficult to install on our landscapes, and it has taken a persistent and focused effort to make it possible. However, utilizing some Northwest timber sales to learn how to better achieve ecosystem management seems altogether appropriate. We share our perspectives on implementing large-scale experiments in the sections that follow.

*1. **DEMO and adaptive management.*** The information obtained from studies such as DEMO can provide the ecological or sociological basis for modifying our management practices over time. Under the Northwest Forest Plan, timber will continue to be harvested from several million acres of public land in the Pacific Northwest. However, the consequences of varying levels and patterns of green-tree retention in regeneration harvests have not been systematically examined. The DEMO study will test some of the assumptions used to formulate the Northwest Forest Plan and its associated standards and guidelines. Where appropriate, the information can also be used by local managers to meet resource objectives that are formulated by interdisciplinary teams at the project level.

So that future management can be more effective, we will need to provide specific examples of how the information obtained from DEMO can be used to design new silvicultural regimes, and guidance on how related harvest practices might influence forest function. The greatest challenge in DEMO is to tangibly link study results to decision support tools for forest management.

*2. **Large-scale interdisciplinary studies have benefits and limits.*** One of the potentially strong points of the DEMO study is that it encompasses both biological and social investigations and attempts to integrate among these. For example, wildlife investigators are providing fecal material from trapped small mammals to investigators of fungal communities. Jointly, researchers are examining which species of fungi are consumed by small mammals, and how these relationships vary with the relative abundance of fungi, thus providing insight into food web relationships (see Cazares et al. 1999). Similarly, vegetation studies (Halpern et al. 1999) will provide information on the changes in forest composition and structure that may drive many of the responses of the other organisms and ecosystem processes being investigated. However, multi-disciplinary studies may have limitations. Legal and managerial requirements for conducting timber harvests on National Forests make installation of large, complex experiments particularly difficult, and may constrain designs that would satisfy multiple research objectives.

*3. **Long-term planning**.* Large-scale silvicultural or ecological experiments, placed on public lands that are managed at least partly for timber production, require comprehensive planning prior to initiation. National Forests and other cooperating agencies should be included in planning activities from the outset. Large-scale experiments involve numerous considerations to ensure that they can actually be implemented.

*4. **The greatest value may be long-term in nature**.* Large-scale harvest experiments such as DEMO may provide their greatest value in decades to come. Initial results will indicate the immediate changes due to treatments, but long-term results may be more relevant than short-term responses to disturbance. Managers and scientists encourage maintenance of study sites and sampling grids for this long-term work.

However, any long-term study on actively-managed lands, rather than in research natural areas or experimental forests, presents difficulties. For example, adjacent or nearby harvests may influence study sites. The participating National Forests have committed not to harvest the study sites in the future. Sites will be protected from wildfire as much as possible, but there is the possibility of future disturbances from fire, wind, or pathogens. The possibility of future stand treatments, e.g., precommercial thinning of young trees, will be addressed over time. Long-term maintenance of the DEMO study will require ongoing commitment and effort from both managers and scientists. From our perspective, the value of maintaining this large experiment, with its potential wealth of information, is worth the effort.

*5. **Collaboration with scientists on public lands**.* A major benefit that can result from

experiments such as DEMO is the resulting collaboration between participating managers and scientists. One benefit of collaboration is simply the increased interaction between managers and scientists, sharing past experiences, results of other research, and future desires. Collaboration has been essential to the planning of the DEMO study to ensure that we prepare a scientifically valid, yet feasible study. Collaboration with Oregon State University and the University of Washington has attracted additional research to DEMO sites, that has culminated in a number of graduate theses (e.g., Pipp 1998). In addition, ancillary research is being performed at other sites on the Diamond Lake Ranger District, Umpqua National Forest, as the result of DEMO-related connections with local managers. Findings from such research hold the promise of providing assistance to local managers in future projects.

6. Studies provide increased local information. A great value of experiments such as DEMO is the increased level of local knowledge they afford. Pre-harvest sampling on DEMO sites has provided the two National Forests and DNR with a wealth of information about these specific sites. Species lists for vascular and non-vascular plants, birds, small mammals, flying squirrels, bats, fungi, and amphibians provide much more detail than we normally gather in Forest monitoring and project planning activities. Longer-term results should be even more valuable.

7. Participation. Public participation is essential in designing large harvest studies. Virtually all timber harvesting on public lands is controversial to some degree; timber harvests designed as experiments bring additional complications. Some welcome the idea that we may gather information from harvests that will enable us to improve future work. Others are concerned by the limited flexibility to mitigate problems. Much time needs to be invested in describing standard experimental procedures such as the need for random assignment of treatments.

It is important that scientists are an integral part of public involvement. Project scientists can better describe the rationale for study designs than can managers, and the public usually expects to hear from scientists as well as project managers. Participation in this process also helps scientists better understand public concerns and expectations.

A common concern raised during implementation of the DEMO study has been its longevity. Many people question the resolve of scientists and managers to carry out long-term research. Given annualized budgeting and decreasing federal budgets, most federally-sponsored researchers are in no position to provide guarantees. Indications of support, such as the memorandum of understanding for DEMO between the Pacific Northwest Region and the Pacific Northwest Experiment Station, can help to show intent. It is equally important, however, to be honest about the uncertainty of continued funding.

Concluding Thoughts

The design, planning, and implementation of the DEMO study has involved ongoing discussion and compromise among managers and scientists. The experimental design is intended to reduce extraneous variation, and to increase our ability to detect how forest ecosystems respond to varying levels and patterns of green-tree retention. In the process, however, this experimental design has led to unconventional types of timber sales, and may therefore produce unanticipated results. The scientists and managers involved understand these limitations, as well as the rewards that large-scale interdisciplinary studies may provide.

Although post-harvest sampling is just beginning, we have learned a great deal about implementing large-scale experiments, gathered a wealth of information about DEMO sites, and learned about interaction and collaboration between science and management. Although the rigidity required of scientific study may conflict with desires of forest management, it takes collaboration and compromise between managers and scientists to design and implement studies of this magnitude and scope.

Acknowledgements

We thank Don Ostby, Claude McLean, Jon Nakae, Dave Hibbs, Robert Ribe, Richard Bigley and Wayne Kleckner for their reviews of earlier drafts of this paper. Special thanks to Cindi Lagoudakis, Debbie Anderson, Wayne Kleckner, and Barbara Fontaine (Umpqua National Forest); Richard Bigley (Washington DNR); and Debbie Couche, Jon Nakae, Ed Tompkins, and Sue Macmeeken (Gifford Pinchot National Forest) for their ideas

and suggestions, and for their hard work over the past several years. This is a product of the Demonstration of Ecosystem Management Options (DEMO) study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources.

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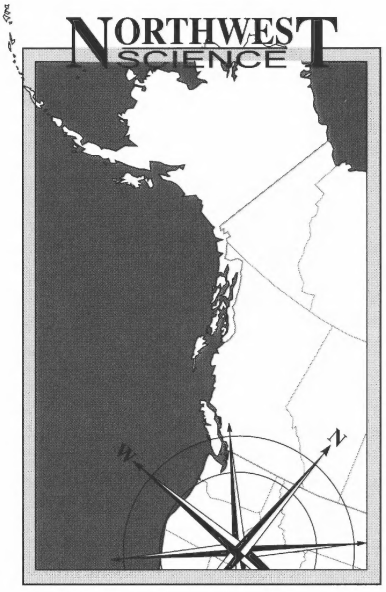

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